ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XVIII   No. 1

GENERIC RELATIONSHIPS OF THE DOLICHOPODIDAE (DIPTERA)

BASED ON A STUDY OF THE MOUTH PARTS

WITH THIRTY PLATES

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ACKNOWLEDGMENTS

INTRODUCTION

A REVIEW of the literature on the mouth parts of Diptera shows that exhaustive morphological studies have been made on only a few species such as that on Culex by Dimmock (1881, 1882) and on the proboscis of Musca by Kraepelin (1882, 1883). Comparative studies of the mouth parts of many genera and families are presented by Menzbier (1880), Langhoffer (1901), Becher (1882), Meinert (1882), Smith (1890), Kellogg (1899), Wesché (1904), Peterson (1916), and Frey (1921). So far as the family Dolichopodidae is concerned (with the exception of Langhoffer's work, 1901), only scattered references to the study of the mouth parts are to be found in Becher (1882), Smith (1890), Wesché (1904), Lundbeck (1912), Snodgrass (1922), and Williams (1939).

Interest in Langhoffer's grouping (1901) of the Dolichopodidae on the basis of mouth parts, and the work of Snodgrass (1922) on the mouth parts of *Melanderia mandibulata* Aldr. prompted this investigation. The writer was curious to ascertain if the groupings of the American genera on the basis of mouth parts would conform to those of Langhoffer.

According to previous investigators, Loew (1864), Packard (1870), Kleine (1907), Williston (1908), Lundbeck (1912), Howard, Dyar, and Knab (1912), Malloch (1917), Lutz (1918), Aldrich (1922), Comstock (1924), Imms (1934), Curran (1934), Snodgrass (1935), Tillyard (1936), and Williams (1938), all adult Dolichopodidae are predaceous. The trophi, therefore, are not only able to seize the prey, but also to hold and to grind it. The masticated food is then transferred to the mouth aperture, which is located between the bases of the labrum and the hypopharynx. A pharyngeal sack (Figs. 192, 193), lying on the inner wall of the pharynx and connected with the mouth aperture, conveys the food to the oesophagus.

In order to reach a correct interpretation of the structure of the mouth parts, each part, regardless of the systematic position of the various genera accorded by previous workers, was carefully studied, and then compared with other similar parts. On the basis of the comparative study of all the parts the type groupings described below were established.

The adult feeding mechanism of the dipterous family Dolichopodidae forms a compact group of structures projecting downward from the clypeopharyngeal region of the head. Some of these parts are retracted, and they require preparation and dissection before their structures can be observed. Four different types of mouth parts were found to occur in the family. These I have termed: (1) the labralate, or Diaphorus, type; (2) the epipharyngeal two-prong,[1] or Medeterus, type; (3) the

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[1] Snodgrass (1922, p. 149) uses the word *prong* in describing *Melanderia mandibulata* Aldr.

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epipharyngeal four-prong, or Melanderia, type; and (4) the epipharyngeal plate,[2] or Dolichopus, type.

All types are made up of the labrum, with a strongly developed epipharyngeal armature[3] and an apodeme, hypopharynx, paired maxillary palpi, and a labium, which bears a pair of labella at its distal end. On each labellum five or six radiating pseudotracheae are present.

The terms applied to the various parts are those commonly used in entomological literature. Regarding the terms of the labrum, the nomenclature of Snodgrass has been followed. The drawings are all freehand sketches and mostly made under high dry or oil immersion lenses. An attempt has been made not only to show the characteristic features involved in the isolated part, but also to show the relation of all the parts to one another.

MATERIALS

CURRAN (1934) in his "North American Diptera" lists sixty-two genera in the family Dolichopodidae; of these, thirty-two have been secured by the writer and dissected for the investigation. The males and females of many species have been observed. The following representatives of the various genera have been studied; those from which drawings have been made are indicated by an asterisk.

Aphrosylus praedator Wheel., female* (Figs. 14, 39, 71, 98, 142a, 142b, 173)
Argyra albicans Lw., female* (Figs. 29, 54, 86, 113, 158, 189)
Campsicnemus nigripes V.D., female and male* (Figs. 15, 52, 84, 111, 143, 174)
Campsicnemus thersites Wheel., male
Chrysotus choricus Wheel., male* (Figs. 16, 34, 66, 105, 144, 175)
Chrysotus obliquus Lw., female
Condylostylus sipho Say, female* (Figs. 1, 45, 77, 97, 129, 160)
Diaphorus leucostomus Lw., male* (Figs. 17, 33, 65, 103, 145, 176)
Diostracus prasinus Lw., male and female* (Figs. 9, 43, 75, 121, 137, 168)
Dolichopus bifractus Lw., male
Dolichopus consanguineus Wheel., female
Dolichopus cuprinus Wied., female and male
Dolichopus longipennis Lw., female
Dolichopus plumipes Scop., female
Dolichopus ramifer Lw., male and female* (Figs. 27, 64, 96, 115, 155, 186, 191, 192)
Dolichopus scapularis Lw., male and female
Dolichopus vittatus Lw., female
Gymnopternus barbatulus Lw., male* (Figs. 10, 62, 94, 122, 138, 169)
Hydrophorus aestuum Lw., male and female
Hydrophorus sodalis Wheel., male and female* (Figs. 13, 51, 83, 128a, 128b, 141, 172)
Hygroceleuthus consanguineus Wheel., female and male* (Figs. 28, 63, 95, 116, 156, 187)
Hypocharassus pruinosus Wheel., male and female* (Figs. 8, 49, 81, 118, 136, 167)
Laxina calcarata Lw., female and male* (Figs. 2, 44, 76, 101, 130, 161)
Laxina patibulatus Say, female and male

[2] Langhoffer (1901, p. 843) uses the word *platta*.
[3] Snodgrass (1935, p. 317), in *Principles of Insect Morphology*, states: "The posterior surface of the dipterous labrum is smooth and presents no structure of any kind to be specifically termed an epipharynx. The writer sees no reason for following the usual custom of calling the elongated labral lobe of Diptera a labrum-epipharynx."

Liancalus hydrophilus Aldr., female and male
Liancalus similis Aldr., male* (Figs. 23, 53, 85a, 85b, 114, 151, 182)
Medeterus aldrichi Wheel., male* (Figs. 6, 37, 69, 110a, 110b, 134, 165)
Medeterus vittatus V. D., male and female
Melanderia mandibulata Aldr., male* (Figs. 32, 50, 82, 119, 159a, 159b, 190)
Mesorhaga sp., female* (Figs. 31, 47, 79, 125)
Millardia intentus Aldr., male and female* (Figs. 12, 41, 73, 126, 140, 171)
Neurigona carbonifer Lw., male and female* (Figs. 18, 36, 68, 100, 146, 177)
Neurigona pectoralis Lw., female and male
Neurigona rubella Lw., female and male
Pelastoneurus vagans Lw., male and female* (Figs. 24, 60, 92, 123, 152, 183)
Peloropeodes acuticornis V. D., female and male* (Figs. 20, 55, 87, 117, 148, 179)
Plagioneurus univittatus Lw., male and female* (Figs. 19, 58, 90, 112, 147, 178)
Rhaphium effilatus Wheel., female and male* (Figs. 7, 35, 67, 102, 135, 166)
Scellus exustus Walk., male
Scellus filiferus Lw., male and female* (Figs. 26, 40, 72, 127, 154, 185, 193)
Scellus monstrosus O. S., male and female
Sciapus scintillans Lw., male and female* (Figs. 4, 46, 78, 124, 132, 163)
Sympycnus frontalis Lw., female
Sympycnus lineatus Lw., male* (Figs. 22, 61, 93, 106, 150, 181)
Syntormon cinereiventris Lw., female and male* (Figs. 21, 59, 91, 104, 149, 180)
Tachytrechus angustipennis Lw., male and female* (Figs. 25, 57, 89, 109, 153, 184)
Teuchophorus spinigerellus Zett., female* (Figs. 30, 56, 88, 107, 157, 188)
Thinophilus ochrifacies V. D., female and male* (Figs. 11, 48, 80, 120, 139, 170)
Thrypticus willistoni Wheel., female and male* (Figs. 5, 38, 70, 108, 133, 164)
Xanthochlorus helvinus Lw., female* (Figs. 3, 42, 74, 99, 131, 162)

METHODS OF PROCEDURE

Dried, pinned specimens were used for study. In order to make the investigation as comprehensive as possible, one or more of the representative species of each genus were used. Males and females were examined; but the mouth parts of only one sex in each species are figured since there are no great sexual differences in the mouth parts.

After each specimen was properly labeled, the head was removed and placed on a piece of cotton, which was plugged into a three-inch piece of glass tubing, resembling a small vial. When the desired number of vials had been prepared, they were placed, cotton end downward, in a beaker which contained a ten per cent solution of potassium hydroxide. After the solution had arisen in each vial, and each head was properly enveloped, the other end of the vial was also plugged. This precaution was taken to prevent the entrance of foreign matter. The specimens were left in the solution for twenty-four hours. The vials were then transferred to another beaker and washed in three or four changes of distilled water, in order to remove the potassium hydroxide. Each head was then transferred by means of a camel's hair brush to a deep-welled culture, or hanging drop, microscope slide. Dehydration was carried on in 30, 50, and 75 per cent alcohol. The mouth parts were dissected from the head in 75 per cent alcohol and further dehydrated in 85 per cent, 95 per cent,

and absolute alcohol. The specimens were then cleared in xylol and mounted in glycerine. When the study of the toto mouth parts had been completed, the individual mouth parts were then dissected in glycerine under a binocular microscope. The parts were placed separately on regular microscope slides and again mounted in glycerine. The parts were then studied with the aid of a compound research microscope. Some structures were so minute that high-power dry lenses, and often oil-immersion lenses, had to be used.

FAMILY CHARACTERISTICS, HABITATS, AND FOOD HABITS

THE FAMILY Dolichopodidae is one of the higher families of the Brachycera series of the suborder Orthorrhapha. They are tiny, attractive, slender flies having hemispherical, elongated heads, generally wider in the female than in the male. The eyes are large, hairy, and more or less oval in shape, and in the living specimens they are a metallic green, with reddish or purplish reflexes. The three-segmented antennae are inserted near to each other, above the middle of the eyes. The third segment of the antennae is sometimes elongated in the male. A dorsal or apical arista is also present. The maxillary palpi are flat and are unsegmented. They are usually bristled and generally rest on the protruding mouth structures. The flies are iridescent green or blue-green in color. Some species, however, are brown, yellow, and sometimes black. The brisk, restless, little creatures have legs that are much longer than is usual in the families belonging to the series. Hence the name Dolichopodidae (long-footed) is applied to the family.

The venation of the wing is so peculiar that it in itself is sufficient to distinguish the Dolichopodidae from their nearest allies. The absence of a cross vein between the discal cell and the second basal cell is very evident. Cells M and 1st M_2 are therefore not separated, but united to form one large single cell. The anal cell is short, the sixth vein is also short or absent, and the fourth vein is usually straight or gently curved. The characteristic venation is sufficient to distinguish the family.

Sexual dimorphism is quite pronounced in this group of flies. Secondary sexual characteristics of the male occur in the tarsi, tibiae, femora, wing apex, in the third joint of antennae, arista, and palpi. The hypopygium may be large, or small and concealed. The males are therefore easily distinguished. According to Curran (1934, p. 216), the females are often difficult to name, as they present less striking characteristics than the males. Lutz (1918, p. 252) states that the number of described species of Dolichopodidae is increasing rapidly, and the end is not yet in sight.

The members of this family are commonly distributed. They are

generally found in the neighborhood of water. Miall (1934) tells us that "the naturalist, in search of aquatic insects, cannot fail to find them almost daily and hourly, sometimes in swarms, sometimes singly. They come to rest on the grasses, herbs, or bushes near to water, on stones in the beds of streams, or even on the surface of the water itself. Some rival the pond-skaters (Gerridae, Hemiptera) in the agility with which they dart to and fro upon the surface of rapid streams; others hover incessantly in the spray of waterfalls."

Several genera of this brilliantly colored, raptorial group haunt the surf and breakers of the seashore. Hydrophorus, "the water skater" (Williams, 1939, p. 307), is found in maritime marshes bestraddling the water of muddy shallows or exploring the oozy ground of their vicinity. It propels itself entirely by strong simultaneous strokes of its far-spreading middle legs. The name Hydrophorus was bestowed upon these insects, because of the ability of many of the species to run, even upon agitated water (Loew, 1864, p. 211). Thinophilus (Schiner, 1862), Melanderia (Aldrich, 1922), and Hypocharassus (Williston, 1908) live principally along the shores of the sea. The small, shiny, species of Sympycnus are also seashore lovers. Syntormon (Parent, 1938) may be found on the wet rocks of brackish waters. The gregarious species of Aphrosylus are seen flitting about in the spray of the breakers, among seaweed. The name of this genus has reference to the habit of these species of pursuing their prey along the shores of a surging sea (Loew, 1864, p. 148).

The beautiful, silvery species of Argyra establish themselves in the vicinity of fresh water brooks. The females are often found resting on leaves. The name of this genus has reference to the beautiful, silvery luster of most of the species (Loew, 1864, p. 124). The lively species of Tachytrechus are found often resting on the boards of dams, near clear, sandy brooks (Schiner, 1862). The name of the genus, meaning "I run," has reference to the habit of many species of running along sandy and muddy banks (Loew, 1864, p. 110).

The terrestrial individuals of Dolichopodidae may be found on tree trunks, meadow-grass, leaves of shrubs, damp localities, and rocks. Sciapus, Neurigona, and Medeterus are found on tree trunks. Diaphorus may be found on the leaves of shrubbery in company with the agile little species of Chrysotus. The name of the genus Chrysotus has reference to the gold-green color of many species (Loew, p. 172). Scellus is collected by beating about the grass of low meadows (Aldrich, 1907). Plagioneurus is collected in similar places (Wheeler, 1899). The beautiful, yellow genus Xanthochlorus is found in damp places on high vegetation, and on low shrubs (Schiner, 1862). Gymnopternus is found, with the oldest and largest genus, Dolichopus, in damp places, on banks of brooks, and near water puddles. Liancalus prefers the rocks in cold, wet

places (Williston, 1908). Rhaphium is found on the leaves of plants of forest rivulets (Schiner, 1862).

The species of Campsicnemus are widely distributed. Many occur on paths and on the leaf-littered forest floor; others walk or skate upon the surface of puddles, and others still are found on the leaves of plants, where they may be exposed to sunlight. In humid regions small numbers patronize the stems of bananas (Williams, 1938). The name of this genus was given because the males of many species are distinguished by the peculiar curvature of the middle tibiae (Loew, p. 193).

This large family of carnivorous flies, as adults, prey on other insects. According to Comstock (1924) the flies prey upon weaker insects. Miall (1934) says at least one species of Dolichopodidae preys upon certain species of Podura, and it is probable that many flies, freshly hatched from a variety of aquatic pupae, fall victims to these swift and destructive enemies. Lutz (1918) maintains that the adults are all predaceous, capturing chiefly the minute, soft-bodied flies. Packard (1870) describes the flies as predatory on other insects. Aldrich (1922) states they capture the smaller, weaker flies, and in their favorite haunts at the edge of the water they pick up small chironomid and other dipterous larvae, as well as oligochaete worms.

Williams (1938) states that Collembola seem to be the chief food of *Campsicnemus funipennis* Parent, which also feed on drosophilids attracted to decaying bananas. Gründberg (1910) described the flies as robbers on small insects.

Howard, Dyar, and Knab (1912) say that Dr. Paul Osterhout, of Panama, has observed flies of the family Dolichopodidae, well known for their predaceous habits, attacking mosquito larvae. They quote the following from his letter to the Surgeon General of Public Health and Marine Hospital Service: "A short time ago, in passing through the outskirts of the town, I saw a large swarm of small flies seemingly very much occupied about a small pool of water standing in a wagon track (the track had been undisturbed for several days from the appearance), so I stopped to see what the commotion was about and I saw hundreds of these flies and thousands of mosquito larvae. I remained for some time watching the commotion and saw several of the flies catch the larvae and drag them to the dry earth and devour them."

DeLeon (1935), speaking of *Medeterus aldrichi,* says: "Many miscellaneous records mention the finding of larvae and pupae under bark of trees and the observing of adults feeding on some smaller insects . . . . *Medeterus aldrichi* is the most important predator of the mountain pine beetle (*Dendroctonus monticolae* Hopk.) infesting lodgepole and western white pine. It probably destroys 40% - 50% of the brood of this beetle."

Bishop and Hart (1931, p. 152) make the following statement: "In a small gravel pool which derived its water by seepage or overflow from an

adjacent hay meadow, mosquito larvae were extremely abundant. While collecting in this pool our attention was caught by a number of small, metallic-green flies that drifted lightly over the surface of the water or ran rapidly from one resting place to another. On the surface of the pool, the flies were observed to turn first in one direction then another without discernible movement of the legs or wings though the turns seemed well directed and often placed them in position above a mosquito larva or pupa at the surface film. Such movements on the part of flies often cause a precipitous retreat of all the larvae in the vicinity but seldom quickly enough to prevent one of their number being seized and hoisted squirming above the surface. Usually the captive was devoured on the spot, but at times carried away bodily to some convenient perch. After observing the capture of larvae in the field, a number of flies were confined with larvae and pupae in a cheesecloth covered jar partially filled with water. Here the hunting operation could be observed at short range and we saw several captures. The fly in captivity either glided over the surface or suddenly pounced down upon a larva and continued in its flight to a resting place, the mouth parts of the fly alone being involved in seizing the larvae . . . . 93 larvae were devoured in seven days by two small flies . . . . The flies captured while feeding on the surface of the pool were determined for us by Dr. O. A. Johannsen, of Cornell University, as *Dolichopus renidescens, Dolichopus nigricaudo,* and *Dolichopus walkeri.*"

Doane (1907, p. 139), describing the food habits of *Scellus virago* found on the glistening, white, thinly-encrusted salt area bordering San Francisco bay, states: "In its running about it would come close enough to one of the little Agromyzids (*Rhicnoessa parvula* Lw.), that were quite abundant here, pounce upon it and suck its blood. The unfortunate little fly is held and manipulated by the forelegs of its captor, and after being turned over a few times, evidently in order that the blood may be sucked from different parts, the empty skin is dropped to the ground and blown about by the wind, while the vampire goes in search of another morsel."

Williams (1938), describing the food of Hydrophorus, makes the following comment: "It seems that this inhabitant of the sun-beaten lowlands requires occasional refreshment for it will stoop or teeter so as to bring the mouth down to moisture, while food may be wetted in the same manner. No doubt the fly eats many kinds of small organisms floating on water, and it is very fond of 'bloodworms' (the larva of the mosquito-like midge *Chironomus hawaiinsis* Grims) . . . . The bloodworms and flies into which they develop were abundant in and about these shallows. A wandering Hydrophorus fly seized with her tongue-like organ, or labella, a bloodworm that, despite its comparatively large size and vigorous struggles, was hoisted clear out of water and soon quieted.

A little later, a second Hydrophorus stooped down and grasped a blood-worm extricating it from the mud with a final heave. In one of these cases the fly laid hold of the victim with a foreleg—in the laboratory both forelegs were frequently employed to hold small wounded flies."

The writer observed some specimens of *Dolichopus ramifer* Lw., while in captivity in an environment where they had plenty of food, extract tiny annelids from the damp soil. These squirming morsels were held by means of the labella. The fore tibiae aided in holding when the worms became too active. The annelids disappeared in a very short time. They evidently had been all consumed since no remains were visible.

SUBFAMILIES OF THE DOLICHOPODIDAE

THE GENERA of this family have been grouped into subfamilies by various authors:

Classification of Aldrich.—The American genera have been grouped by Aldrich (1905) into the following twelve subfamilies. In a note at the beginning of his work, he says: "The arrangement in subfamilies, much of the synonymy, and some notes, are the result of my own study of the family, which has been a favorite with me for fourteen years."

I. AGONOSOMINAE
Psilopodinus
Agonosoma
Mesorhaga
Leptorhethum

II. DIAPHORINAE
Diaphorus
Asyndetus
Chrysotus
Eutarsus
Teuchophorus
Campsicnemus

III. RHAPHIINAE
Argyra
Leucostola
Porphyrops
Rhaphium
Nematoproctus
Syntormon

IV. SYMPYCNINAE
Parasyntormon
Sympycnus
Nothosympycnus
Anepsiomyia

V. NEURIGONINAE
Neurigona

VI. XANTHOCHLORINAE
Achalcus
Chrysotimus
Xanthochlorus
Xanthina

VII. THINOPHILINAE
Thinophilus
Diostracus
Hypocharassus
Phylarchus

VIII. MEDETERINAE
Medeterus
Peloropeodes
Thrypticus
Coeloglutus

IX. HYDROPHORINAE
Hydrophorus
Scellus
Liancalus

X. PLAGIONEURINAE
Plagioneurus

XI. APHROSYLINAE
Aphrosylus

XII. DOLICHOPINAE

Dolichopus	Polymedon
Gymnopternus	Sarcionus
Hercostomus	Pelastoneurus
Paraclius	Leptocorypha
Tachytrechus	Orthochile

Classification of Lundbeck.—The classification of Aldrich has been criticized by Lundbeck (1912), who follows the subfamily divisions of Kertesz (1909). Why he does so is suggested in his remarks which follow: "The subdivisions of family of Dolichopodidae in subfamilies is at present not satisfactory, at all events with regard to the palaearctic fauna. In the Kat. paläarkt. Dipt. the family is divided into four subfamilies. With regard to the American fauna Aldrich (A Cat. of North Am. Dipt., Smiths. Misc. Coll. XLVI, 1905) has divided the family into not less than twelve subfamilies; these are, I think, good and natural, but the author has given no diagnosis of them. As I have only examined the Danish genera and species more closely, I have thought more advisable at present to keep the subfamilies given in the Kat. paläarkt. Dipt., though I am well aware, that some of them are no doubt somewhat heterogeneous. I have only made few alterations . . . . I have placed Thrypticus and Acropsilus . . . . in the Hydrophorinae, the former near Medeterus, the latter near Thinophilus and Schoenophilus. The experienced Dipterologist, Mr. T. Becker in Liegnitz, to whom I am indebted for many valuable hints, works at present with the Dolichopodidae, and we may hope soon to have from his hand a new and more satisfactory arrangement of the family in subfamilies."

Classification of Becker.—For the purpose of comparison with the arrangements previously made and with those worked out in the present study, Becker's (1922) classification of the genera in nearctic and neotropical regions is given:

I. DOLICHOPODINAE

Dolichopus Latr.
Hygroceleuthus Lw.
Hercostomus Lw.
Paraclius Big.
Pelastoneurus Lw.
Sarcionus Aldr.
Stenopygium Becker
Tachytrechus Walk.
Polymedon O. S.
Macellocerus Mik.
Psilichium Becker
Sybistroma Meig.
Leptocorypha Aldr.
Gonioneurum Becker

II. PLAGIONEURINAE

Plagioneurus Lw.

III. HYDROPHORINAE

Hydrophorus Fall.
Scellus Lw.
Liancalus Lw.
Thinophilus Walk.
Diostracus Lw.
Hypocharassus Mik.
Syntomoneurum Becker
Phylarchus Aldr.
Peodes Lw.

IV. APHROSYLINAE

Paraphrosylus Becker

V. MEDETERINAE

Medeterus Fisch.
Thrypticus Gerst.

VI. RHAPHIINAE
Rhaphium Meig.
Porphyrops Meig.
Xiphandrium Lw.
Syntormon Lw.
Eutarsus Lw.
Achalcus Lw.
Peloropeodes Wheel.
Systenus Lw.

VII. NEURIGONINAE
Neurigona Rond.

VIII. DIAPHORINAE
Diaphorus Meig.
Lyroneurus Lw.
Chrysotus Meig.
Coeloglutus Aldr.
Asyndetus Lw.
Argyra Meig.
Leucostola Lw.
Achradocera Becker
Symbolia Becker
Xanthina Aldr.

IX. STOLIDOSOMINAE
Stolidosoma Becker

X. CAMPSICNEMINAE
Campsicnemus Halid.
Sympycnus Lw.
Subsympycnus Becker
Hyptiochaeta Becker
Calyxochaetus Big.
Chrysotimus Lw.
Xanthochlorus Lw.
Anepsiomyia Bezzi.
Teuchophorus Lw.

XI. CHRYSOSOMATINAE
Condylostylus Big.
Megistostylus Big.
Mesorhaga Schin.
Leptorhethum Aldr.
Sciapus Zell.

XII. Genus *incertae sedis*
Anchineura Thoms.

This arrangement by Becker is based mostly on the following external characters and shows that the mouth parts have been given no consideration:

Dolichopodinae.—The first joint of the antennae is pubescent on the dorsal surface.

Plagioneurinae.—The hypopygium lies completely imbedded in the sixth abdominal segment. The shape and arrangements of the organs of the hypopygium are remarkable and find no analogy in this family.

Hydrophorinae.—No special characteristics are given by Becker, but this statement is translated from his work: "Of our palearctic genera we can name four which America shares with us: Hydrophorus, Scellus, Thinophilus, and Liancalus. Besides, America has three genera which do not occur with us: Diostracus (Lw.), Hypocharassus (Mik.), and Syntomoneurum n. genus. Also are listed: Phylarchus (Aldr.), a new genus placed in the Thinophilinae by Aldrich, and Peodes (Lw.), which is mentioned by Bigot; furthermore, Peloropeodes (Wheel.) is found in Kertesz' catalogue with the Hydrophorinae, in Aldrich's catalogue with the Medeterinae. I can place this latter genus only with the Rhaphiinae."

Aphrosylinae.—The palearctic species have almost a totally bare thorax on which stand only four pairs of dorsal medial bristles; the coxae have short thornlike bristles, and the trochanters carry two strong, diverging bristles. The antennae of the American species are quite small. Those of the male are much smaller than those of the female.

Medeterinae.—No characteristics are given, but Becker states that the only American genera in this subfamily are Medeterus and Thrypticus.

Rhaphiinae.—According to Becker this group is represented in the palearctic zone by ten different genera; but at the present time the American fauna has fewer genera. Besides our three main genera, Rhaphium, Porphyrops, and Syntormon, only Xiphandrium and Achalcus and perhaps Peloropeodes are to be included here.

Neurigoninae.—No characteristic is given for this group and only one genus, Neurigona, is placed in it.

Diaphorinae.—Diaphorus (Meig.), Chrysotus (Meig.), Asyndetus (Lw.), Argyra (Macq.), and Leucostola (Lw.) occur in North America. Lyroneurus (Lw.), and the two new genera, Achradocera and Symbolia, are established in South America. No characteristics were given.

Campsicneminae.—Thirteen genera of this group are recognized in the palearctic region, while only eight genera are found in the nearctic and neotropical regions. These are: Sympycnus (Lw.), Chrysotimus (Lw.), Anepsiomyia (Bezzi), Teuchophorus (Lw.), Subsympycnus (Beck.), Hyptiochaeta (Beck.), and Calyxochaetus (Big.). The dominating genus is decidedly Sympycnus.

Chrysosomatinae.—Five different genera belong here. The dominating genus is Condylostylus. It has a dorsal antennal bristle. In most species the wings show two diagonal stripes connected on the front margin. Sciapus has a very limited number of species and is very similar to Condylostylus. The genus Leptorhethum, established by Aldrich (1893), is closely related to Sciopus and differs only through a narrower head and a less deepened frons. A fourth genus, Mesorhaga, was introduced by Schiner in 1862. The members of this genus have the third antennal joint drawn out in the shape of a cone without any visible separation from the long, apical, antennal bristle.

Classification of Curran.—The family Dolichopodidae is called by Curran (1934) "Dolichopidae" and "long-headed flies." He does not group the genera into subfamilies and recognizes sixty-two American genera. He comments: "The American species were revised by Becker but so many new forms have been described since that this work will furnish only a basis for the study of the family."

MOUTH PARTS OF THE DOLICHOPODIDAE

AMONG the previous studies of the mouth parts of this family, the work of Langhoffer (1901) deserves first consideration because he proposed a grouping of the genera which prepared the way for the present study.

Langhoffer's Study.—The importance of the mouth parts as diagnostic characters in a natural arrangement of the genera of the Dolichopodidae was first indicated by Langhoffer in 1901 when he proposed the four following groups:

First Group (Type Hydrophorus). Here are classified forms in which two long hooks or tusk-like prongs project beneath the labrum (Langhoffer, Fig. 1, p. 843). The following genera are placed in this group: Medeterus Zitt., Hydrophorus Fall., Liancalus L., Tachytrechus Walk., Psilopus F., Thinophilus Zitt., Aphrosylus Lw., Campsicnemus Fill., Machaerium Lw., Xanthochlorus W., Sympycnus Meig., Chrysotus Meig., Argyra F.

Second Group (Type Dolichopus). The epipharyngeal armature is less strongly chitinized than in the first group, and it is a light-brown color under the microscope. It consists of two longitudinal denticulated plates, which are placed under the labrum and end in tooth-like structures (Langhoffer, Fig. 2, p. 843). Here are grouped: Dolichopus Deg., Gymnop-

ternus Fill., Syntormon F., Hygroceleuthus Hal., Teuchophorus Kow., Diaphorus Meig.

Third Group (Type Porphyrops). The epipharyngeal armature in this group is long, narrow, and richly set with tooth-like bristles (Langhoffer, Fig. 3, p. 844). It is very much weaker than in the first two groups. Only one genus is put in this group: Porphyrops Lw.

Fourth Group (Type Orthochile). All the mouth parts of this group are long and narrow, even the maxillary palpi. Under the labrum are narrow, weak "mandibles," rounded at their distal ends. There are no tooth-like bristles, only here and there a few small setae (Langhoffer, Fig. 4, page 844). Two genera are placed in this group: Neurigona Rond. and Orthochile Lw.

Other Studies.—The mouth parts of this family have also been studied to some extent by the following investigators: Becher (1882), Smith (1890), Wesché (1904), Lundbeck (1912), Snodgrass (1922), and Williams (1939). Their findings will be reviewed here before the present writer's observations are presented.

Becher (1882, p. 148) described the mouth parts as follows: The proboscis is short and strong, and projects only slightly out of the oral cavity; but the distal parts can be moved against each other, as in other families. The maxillae appear to be absent, and only the palpi seem to exist. These are oval in form, with a long bristle at the tip. They rest on the proboscis. The labrum does not serve here, as elsewhere, as a covering of the upper parts, but it is a true chewing apparatus. In consequence of its great movement, and its form, it is used in the grinding of food. This can be observed in the living animal. Since the Dolichopodidae actually chew their food—small insects—the labrum is in constant action. A short dagger-like stylet lies under the labrum. It is broad at its proximal end, where the duct of the salivary glands opens into it. The labium consists of a medianly divided mentum and the lateral chitinous rods (stipes) of the upper plate. These rods go to the labella. The labella are capable of movement one upon the other. In this way they crush the insects that get between them. The effect of this grinding power is increased because the inner lips carry five or six radiating, grinding panels. In Medeterus the proboscis is thicker than in Dolichopus. The form is similar to Dolichopus. The species of Orthochile have a long Empis-like proboscis. Becher shows a lateral view of the entire mouth parts of *Dolichopus aeneus* Deg. in his Plate III, Fig. 16. In this same plate, Fig. 15a is a lateral view of the hypopharynx of Medeterus sp., and Fig. 15b is a cephalic view of the same structure.

Smith (1890, p. 344) recorded the following: "Some specimens of a Dolichopid prepared for examination proved failures, owing to the lack of differentiation in the mounted material, and only a very unique char-

acter of the galear envelope was noted. Instead of pseudo-trachea, or the wrinkled structures often representing it, we find here a series of geminate tubercles decreasing in size from the margin and ending in the membrane. I have not seen this appearance in any other species, and could not study more than the one species of the family from the lack of material." His one figure (p. 335) pictures only four pseudotracheae in a Dolichopid.

Wesché (1904, pp. 28-47) divided the Diptera into eight groups. He placed the family Dolichopodidae in the fourth group because of the following characteristics: The mandibles are fused into the labium; all parts of the maxillae, except the stipes and cardines, are aborted; the palpi present are labial; the tracheae of the paraglossa (labella) are only moderately developed. Furthermore concerning the mouth parts of this family, he made the following statements:

"The mouth parts of the Dolichopodidae possess one feature which separates them from all other families in Diptera: the tracheae on the paraglossa are of the most curious description. Under high powers, each one of them appears to be made up of a number of sub-rectangular semi-transparent cells, which decrease in size as the tracheae approaches the edge of the labellum; at its extremity is a very short, blunt hair inserted in a minute cylinder. In *Medeterus truncorum* Mg., it has another appearance, rather granular and less differentiated. In most genera of this family the cardines of the maxillae are very anteriorly placed—the points on which the palpi are usually situated (close to the base of the labrum) are quite at the extremity of the paraglossae, and have feathered processes at the extremities, which are probably the remains of the maxillary palpi. The mentum has a central rod, which ends in a point between the paraglossae; this rod has a median suture, and is homologous with the paired rods found in Bibio, and the ventral apodeme in Tipula, and represents the mandibles. This character is found in several families, and marks them off from the Muscidae, where the mandibles are on the dorsal side of the labium. The labrum is elaborately toothed and haired, and covers a powerful hypopharynx, with a deep channel, connected with a suctorial trachea, the true pharynx. The palpi are single-jointed, with a few long hairs, but with no central sense-organs such as is seen in the second joint of Bibio and of most Nemocera.

"One interesting specialization is found in *Orthochile nigrocerula* Ltr., which has an elongated labium, a totally different arrangement of the cardines, and a general similarity to the mouth parts in the Muscidae. This lengthening of the labium probably enables the insect to reach the nectaries of flowers; most of the other species are raptorial, haunt marshy spots, and feed on minute insects and Gastropods."

Wesché's Plate VI, Figs. 9, 10, 11, 12, 13, and 14, show labrum, hypopharynx, labium, and paraglossa of *Dolichopus griseipennis* Stan.,

in ventral aspect. The pseudotracheae and labial palpi are in dorsal aspect. The trophi of Orthochile Mg. are shown in his Plate VII, Fig. 1.

Lundbeck (1912) gives general descriptions of the proboscis, hypopharynx, and maxillary palpi of Tachytrechus, Argyra, Rhaphium, Xanthochlorus, Medeterus, Dolichopus, Thinophilus, and Neurigona. He does not figure these mouth parts.

Snodgrass (1922, pp. 148-152), in describing the mouth parts of *Melanderia mandibulata* Aldr., points out that the labella have a very unusual development. Each labellum possesses a movable lobe, the terminal part of which is thick, strongly sclerotized, and produced into a large tooth-like structure. These structures are turned inwardly toward each other and give the appearance of mandibles. He says, "Melanderia possesses, besides its pseudo-mandibles, other mouth structures of interest which, however, are not visible externally. There are four great prongs depending from the epipharynx, in addition to the usual hypopharynx, which is a strongly developed, decurved appendage projecting from the lower lip of the mouth within the anterior enclosure of the labium." Six drawings of the different aspects of these structures are figured in his Plate XIV, p. 151. In his *Principles of Insect Morphology* (1935, p. 315), Snodgrass also states, "The only truly, biting flies are certain species of Dolichopodidae in which the terminal lobes of the labium are strongly sclerotized and jaw-like in form and action."

Williams (1938) does not discuss the mouth parts of the Dolichopodidae but illustrates the head of Campsicnemus. His Fig. 18 is a lateral aspect of the head, with labella removed. In this figure he calls the epipharyngeal prongs "maxillae" and "mandibles" respectively. The hairy membrane cephalad of the prongs, and projecting downward, is termed a "labrum-epipharynx." The region proximad of the "labrum-epipharynx" is called the clypeus.

Lateral Aspects of the Entire Mouth Parts.—The lateral aspects of the entire feeding mechanism of the different genera of Dolichopodidae studied by the writer (Figs. 1 to 33) present the same general gross features as stated above, with the exception of *Melanderia mandibulata* Aldr. (Fig. 32), already described above by Snodgrass. Typically this mechanism is composed of a large, sclerotized, clypeolabral-pharyngeal region, and a labium. The proximal ridges of the pharynx (Fig. 1, *ph*) are deeply invaginated and end in two projections, the cornuae (Fig. 1, *cu*). The clypeus (Fig. 1, *c*), anterior to and fused with the pharynx, is always pubescent. The labrum (Fig. 1, *l*), distad of the clypeus, is usually rounded. It sometimes possesses a membranous flap-like projection as in Laxina (Fig. 44). The maxillary palpi (Fig. 1, *mx.p*, and Fig. 191), are oval in shape. The exact point of insertion is difficult to determine because at one time they seem attached to the clypeolabral region, and at another,

to the labium. They lie on a membranous region between labium and the clypeolabral region (Fig. 191). The hypopharynx (Fig. 1, *hyp*), caudad of the pharynx, has a large salivary bulb (Fig. 1, *s.b*) at its proximal end. The salivary duct (Fig. 1, *s.d*) extends from this bulb to the apex of the hypopharynx. The labium (Fig. 1, *la*) is located caudo-ventrad of the hypopharynx. It is composed of a proximal sclerotized area, the theca (Fig. 1, *t*), and two semimembranous, pilose labella (Fig. 1, *lab*). Pseudo-tracheae (Fig. 1, *ps*) are generally present in each labellum.

Clypeolabral-Pharyngeal Region.—The clypeolabral-pharyngeal region (Figs. 33-65) consists of clypeus (Fig. 33, *c*), labrum (Fig. 33, *l*), pharynx (Fig. 33, *ph*), epipharyngeal armature (Fig. 33, *ep.a*), an apodeme (Fig. 33, *ap*), and a hypopharynx (Fig. 33, *hyp*). In Diaphorus (Fig. 33) the labrum is semitubular and very much elongated. The cornuae are also long. The apodeme is very slender. The salivary bulb at the proximal end of the hypopharynx is rather large. Chrysotus (Fig. 34) has this region similar to that of Diaphorus, but the cornuae are wider. In Rhaphium (Fig. 35) the apodeme is absent, but there is a sclerotized projection extending from the caudal region of the clypeus to the labrum. The hypopharynx is as long as the epipharyngeal prongs. The labrum is not as long as in Diaphorus (Fig. 33), and the cornuae are truncate. The cornuae of Neurigona (Fig. 36) are very small and pointed. The labrum is short and the apodeme broad. The hypopharynx is much longer than the prongs.

The clypeolabral-pharyngeal regions of Medeterus (Fig. 37) and Thrypticus (Fig. 38) differ from the former genera because the prongs are longer and stronger. Both genera have long apodemes and are quite similar, but the prongs and hypopharynx of Thrypticus are at right angles to the pharynx. Aphrosylus (Fig. 39) has a more compact clypeo-labral-pharyngeal region than the preceding genera. The apodeme is very wide, and does not extend beyond the clypeopharyngeal ridges. The hypopharynx is quite long and has a distinct salivary duct leading to the apex. The clypeolabral-pharyngeal regions in Scellus (Fig. 40) and in Millardia (Fig. 41) are very much alike. The cornuae of both are large and high. The apodemes are very wide and their proximal ends are far beyond the clypeopharyngeal ridges. The hypopharynx in each is longer than the epipharyngeal prongs. Scellus has a truncate and piliferous labrum. The cornuae of Xanthochlorus (Fig. 42) are truncate. The apodeme is not broad. Each epipharyngeal prong has a lateral tooth-like structure. In Diostracus (Fig. 43) the prongs have developed a lateral projection to the labrum. The cornuae are rounded. The labrum is longer than that of Xanthochlorus.

Four connected epipharyngeal prongs have developed in Laxina (Fig 44). The labrum has a long, membranous hairy flap at the distal

end. The apodeme is very short and the hypopharynx long. The arrangement of these structures in Condylostylus (Fig. 45) is like that of Laxina, but the apodeme is small. In Sciapus (Fig. 46) and Mesorhaga (Fig. 47) there is also an arrangement similar to Laxina, but in Sciapus the labrum shows a sclerotized prolongation. The anterior pair of prongs in Thinophilus (Fig. 48) have broken up into two pairs of tooth-like structures, which are fused with the labrum by a prolongation from the anterior pair. The apodeme is broad and extends far beyond the clypeopharyngeal ridges. The posterior region of the epipharyngeal armature of Hypocharassus (Fig. 49) has developed into a pair of prongs. The anterior region has become a very efficient lacerating implement. This region has also a pair of prongs, to which is attached broad plate-like processes, possessing a series of small teeth and denticulated edges. The apodeme is broad. Melanderia (Fig. 50) has a not very well differentiated labral region; but it has four well-developed prongs in separable pairs pending from the epipharyngeal area. The hypopharynx is prominent and very long. The apodeme is large and flat. The epipharyngeal arrangement in Hydrophorus (Fig. 51) and in Campsicnemus (Fig. 52) is very similar. The apodemes are very large and rounded at their proximal end. The hypopharynx of the former genus shows a lateral, wing-like flap near the distal end. The anterior, epipharyngeal prongs in Liancalus (Fig. 53) end in two blade-like structures in the labral membrane. The hypopharynx is narrow and very long. The proximal regions of the prongs of Argyra (Fig. 54) and of Peloropeodes (Fig. 55) are plate-like. The clypeopharyngeal region of the latter is wider than that of the former. In Teuchophorus (Fig. 56) the hypopharynx is very long, the apodeme is narrow, and the cornuae are truncate. Tachytrechus (Fig. 57) has wide cornuae. The apodeme is broad. The epipharyngeal structures are more plate-like than in the preceding genera. Plagioneurus (Fig. 58), except for the small cornuae, has a similarly constructed region. The epipharyngeal armature of Syntormon (Fig. 59) consists of denticulated plates. The hypopharynx is very long. Pelastoneurus (Fig. 60) has a very compact clypeopharyngeal region. The labrum is truncate, and the hypopharynx is very long. In Sympycnus (Fig. 61) the labrum is more pointed than in Pelastoneurus. The hypopharynx is long and the apodeme short. In Gymnopternus (Fig. 62) the hypopharynx is more rounded at the apex than that of Sympycnus (Fig. 61). Hygroceleuthus (Fig. 63) has a longer hypopharynx than either Gymnopternus or Sympycnus. Dolichopus (Fig. 64) has a larger apodeme than Hygroceleuthus, and the hypopharynx is also longer.

Epipharyngeal Armature.—The epipharyngeal armature of the Dolichopids (Figs. 65-97) shows modifications in its development. There are present six different forms, which the writer describes as: (1) labrum

elongated with two short prongs, (2) labrum not elongated with two longer prongs, (3) four connected epipharyngeal prongs, (4) four disconnected epipharyngeal prongs, (5) labrum plate-like with four connected prongs, and (6) labrum plate-like with two prongs. The elongated labrum is found in Diaphorus (Fig. 65) and Chrysotus (Fig. 66). In both genera the short tooth-like prongs are fused with the elongated labrum. Rhaphium (Fig. 67), Neurigona (Fig. 68), Medeterus (Fig. 69), Thrypticus (Fig. 70), Aphrosylus (Fig. 71), Scellus (Fig. 72), Millardia (Fig. 73), Xanthochlorus (Fig. 74), and Diostracus (Fig. 75) make up the two-pronged type with a short labrum. The prongs in Rhaphium seem to clasp the labrum. Those of Neurigona are very slender and delicate. In Medeterus and Thrypticus they are long, strong, undenticulated prongs. In Aphrosylus, Scellus, and Millardia the prongs are denticulated. The prongs of Xanthochlorus are decidedly denticulated along the right margin, and there is one prominent tooth-like structure on the left margin of each prong. Diostracus has prongs similar to those of Xanthochlorus.

In the group with four connected prongs are placed Laxina (Fig. 76), Condylostylus (Fig. 77), Sciapus (Fig. 78), Mesorhaga (Fig. 79), and Thinophilus (Fig. 80). The prongs in Laxina, Condylostylus, Sciapus, and Mesorhaga are very similar. In all four genera, the posterior pair of prongs is about twice as long as the anterior pair. Mesorhaga has a projecting structure on each one of the anterior pair of prongs, which is connected with the labrum. The anterior prongs of Thinophilus form a denticular prolongation to the labrum. Hypocharassus (Fig. 81) and Melanderia (Fig. 82) belong to the type with four disconnected prongs. Hypocharassus (Fig. 81) has four acuminate, denticulated prongs carried on one basal plate. The anterior pair consists of plate-like structures, having a series of small teeth. Melanderia has four tusk-like prongs, carried on two basal plates. No denticulation is present on the prongs.

In the group with four connected prongs and a plate-like labrum are placed Hydrophorus (Fig. 83), Campsicnemus (Fig. 84), Liancalus (Figs. 85a and 85b), Argyra (Fig. 86), Peloropeodes (Fig. 87), and Teuchophorus (Fig. 88). In Hydrophorus the posterior pair of prongs is broad and denticulated, while the anterior pair is short and fused with the labrum. The posterior pair of prongs of Campsicnemus is long and denticulated. The anterior pair has a dentate outer edge on each plate. They are fused with the labrum for some distance and end in two short prongs. The posterior pair of prongs of Liancalus is similar to Campsicnemus, but the anterior pair ends in two blade-like structures (Fig. 85b) in a hairy membrane which encloses a denticulated area. The prongs of Argyra are almost similar to those of Liancalus, but they are more plate-like. The anterior prongs are dentate along the outer edges and are fused

with the labrum. Peloropeodes and Teuchophorus have a more plate-like armature than the preceding genera. The posterior prongs are still pronounced, but the anterior pair is fused with the labrum.

The group with a plate-like labrum and two prongs is represented by Tachytrechus (Fig. 89), Plagioneurus (Fig. 90), Syntormon (Fig. 91), Pelastoneurus (Fig. 92), Sympycnus (Fig. 93), Gymnopternus (Fig. 94), Hygroceleuthus (Fig. 95), and Dolichopus (Fig. 96). In Tachytrechus the plates are dentate on the anterior edges, and both posterior corners are dentiform. Plagioneurus resembles Tachytrechus, but the anterior margins of the plates are not so dentate. The plates of Sympycnus, Gymnopternus, Hygroceleuthus, and Dolichopus possess a series of small teeth on their outer surfaces.

Hypopharynx.—The long, tapering hypopharynx of the Dolichopodidae (Fig. 97) is distad of the pharynx and projects beween the lobes of the labella. At its proximal end there is a large salivary bulb (Fig. 97, *s.b*), in the center of which is a dark spot, which seems to be connected with the salivary duct. This duct (Fig. 97, *s.d*) extends the length of the hypopharynx to the apex and seems to parallel a hairy cavity. The shape of the hypopharynx shows a gradual transition from a simple lanceolate type, through a series of triangular, conoidal, sub-quadrately triangular, turbinate, sub-triangular, and pentagonal types.

The lanceolate group is represented by Condylostylus (Fig. 97), Aphrosylus (Fig. 98), Xanthochlorus (Fig. 99), Neurigona (Fig. 100), Laxina (Fig. 101), and Rhaphium (Fig. 102). In Condylostylus the hypopharynx has a distinct salivary duct leading to the apex. It is very narrow. In Aphrosylus we see a similar condition. The hypopharynx of Xanthochlorus is oval at the proximal end, but tapers to a definite point at the distal end. The ventral surface is more modified than that of the preceding genera, and the salivary duct is not so distinct. Neurigona has a hypopharynx that is oval at its proximal end and gradually pointed at its distal end. That of Laxina is similar to Neurigona at its proximal end, but its distal end is abruptly pointed. The salivary duct is also more distinct. Rhaphium has a distinctly wider hypopharynx than any of the preceding genera.

The triangular type of hypopharynx is found in Diaphorus (Fig. 103), Syntormon (Fig. 104), Chrysotus (Fig. 105), Sympycnus (Fig. 106), Teuchophorus (Fig. 107), Thrypticus (Fig. 108), Tachytrechus (Fig. 109), and Medeterus (Fig. 110). In Diaphorus and Syntormon the hypopharyngae are similar, but Syntormon lacks the hairs at the distal end. The hypopharynx of Chrysotus is not so long as that of Diaphorus and Syntormon, and its ventral surface is more complicated. Teuchophorus has a more triangular hypopharynx than Syntormon. The distal end is also more pointed. In Thrypticus the proximal end of the hypopharynx is similar to Teuchophorus, but the apex area is acuminated and curved.

Tachytrechus has a hypopharynx having a general likeness to Thrypticus, but the distal end is not so narrowly curved.

The conoidal type of hypopharynx is found in Campsicnemus (Fig. 111), Plagioneurus (Fig. 112), Argyra (Fig. 113), Liancalus (Fig. 114), Dolichopus (Fig. 115), Hygroceleuthus (Fig. 116), Peloropeodes (Fig. 117), and Hypocharassus (Fig. 118). Campsicnemus and Plagioneurus have similar hypopharyngae, but that of the latter tapers more abruptly toward the distal end. The hypopharynx of Argyra is very broad at the proximal end, then becomes suddenly attenuated to an elongated apex. In Liancalus and Dolichopus the hypopharyngae are narrower at the proximal end than the hypopharynx of the Argyra. Their ventral surfaces are also more modified. Hygroceleuthus and Peloropeodes have the proximal ends and the ventral surfaces of their hypopharyngae more specialized than Dolichopus. The hypopharynx of Hypocharassus is very broad at its proximal end and then suddenly narrows to an elongate, triangular area. The ventral surface is more intricate than any of the preceding genera.

Melanderia (Fig. 119), Thinophilus (Fig. 120), and Diostracus (Fig. 121) have sub-quadrately triangular hypopharyngae. Those of Melanderia and Thinophilus are similar, but that of Thinophilus is longer. In Diostracus the hypopharynx is more pronouncedly sub-quadrate, more suddenly attenuated, and more sharply pointed at the distal end than that of Melanderia and Thinophilus.

The turbinate type of hypopharynx is found in Gymnopternus (Fig. 122) and Pelastoneurus (Fig. 123). Both of these genera have hypopharyngae that are very broad at the base, short, and very pointed at the apex.

The sub-triangular type of hypopharynx occurs in Sciapus (Fig. 124), Mesorhaga (Fig. 125), Millardia (Fig. 126), and Scellus (Fig. 127). These structures are rather narrow at the base and have a short tube-like apex. The hypopharynx of Millardia has hairs at the distal end.

A pentagonal hypopharynx is found in Hydrophorus (Fig. 128a). This appearance is perhaps due to the fact that there is a wing-like flap near the apex (Fig. 128b).

Labium.—The labium (Figs. 129-160) is the only part of the trophi of the Dolichopodidae usually seen on external examination of the mouth part". With the exception of Melanderia (Fig. 159), this structure is r-gularly an elongated, bilaterally symmetrical appendage ending in two oval lobes, known as labella (Fig. 129, *lab*). The membrane (Fig. 129, *m*) investing the oral and distal surfaces of each labellum contains many sensory hairs (Fig. 129, *sh*), which are perhaps tactile in function. Sometimes the external covering of each labellum is strengthened by thin, sclerotized plates (Fig. 130, *sc.p*). Two lateral rods (Fig. 129, *l.r.*)

extend from the pseudotracheal region of each labellum along the sides of the theca. There are no labial palpi. Those figured in the drawings are maxillary palpi. The internal walls of the labella, which are normally in contact with one another, are transversed by pseudotracheae (Fig. 129, *ps*). Rudiments of the glossae (Fig. 129, *g*) are sometimes quite evident. The proximal end of the labium is known as the theca (Fig. 129, *t*). This region is shield-shaped and usually ends proximally in two long projections. Sense hairs are scattered throughout its dorsal surface.

The labium of Condylostylus (Fig. 129) has ribbon-like pseudotracheae. Four blade-like structures, with numerous sense organs, extend from the theca and end in the labellar membrane. In Laxina (Fig. 130) the glossal region forms two pairs of hairy palps. The theca is more bristled than that of Condylostylus. The theca in Xanthochlorus (Fig. 131) has a large bristle on each side. The whole labium is very pilose. Sciapus (Fig. 132) has a labium similar to Laxina, except that the glossal region is not so evident. The labium of Thrypticus (Fig. 133) is very elongated and narrow. In Medeterus (Fig. 134) the labium is larger than in Thrypticus. Rhaphium (Fig. 135) has a labium whose parts are rather difficult to interpret. The theca is small and has a series of bristles. The labella seem to form a canopy from which three or four denticulated pairs of plates descend. The pseudotracheae are peculiar and will be discussed later. In Hypocharassus (Fig. 136) the labium has an ear-shaped sense organ on each labellum. The boundary of the theca was rather difficult to determine. The labia of Diostracus (Fig. 137), Gymnopternus (Fig. 138), and Thinophilus (Fig. 139) are quite similar to Hypocharassus. In Millardia (Fig. 140) and Hydrophorus (Fig. 141), the theca and labella are distinct. A row of bristles appears at the distal end of the theca. Two views of the labium of Aphrosylus are figured (Figs. 142a, 142b). The cephalic view (Fig. 142b) shows two serrate plates with sense organs proximad of the pseudotracheae. The caudal aspect (Fig. 142a) shows hairy lobes proximad of the pseudotracheae. The labium of Campsicnemus (Fig. 143) is very pilose. The labella are short and broad. A bar-like structure is found at the proximal end of the theca of Chrysotus (Fig. 144). The labellar lobes seem to be three-folded. The glossal region is very hairy. Diaphorus (Fig. 145) has a pair of denticulated lobes in the region of the glossae. The labium of Neuιigona (Fig. 146) appears to be tubular. It is rather difficult to define the boundaries of the theca and labella. Plagioneurus (Fig. 147) and Peloropeodes (Fig. 148) have labia similar to Campsicnemus. The theca of Syntormon (Fig. 149) is sub-quadrate. The membranous areas of the labella of Sympycnus (Fig. 150) are larger than those of Peloropeodes, and the glossae are represented by a pair of pilose lobes. The glossal

region of Liancalus (Fig. 151) is also very hairy. Pelastoneurus (Fig. 152) has finger-like structures in each labellum, and the bristles on the theca are crowded at the center of the distal end. Tachytrechus (Fig. 153) has a structure which may be the glossae at the proximal end of the theca, between the labella. Scellus (Fig. 154) has two long projections at the proximal end of the theca, and the lobes of the labella are broad and oval. The labella of Dolichopus (Fig. 155) and Hygroceleuthus (Fig. 156) are broad and very hairy. The theca and labella of Teuchophorus (Fig. 157) are equal in size. Argyra (Fig. 158) has a very large labium. Its theca is greatly indented at the proximal end and has two long proximal processes. The labium of Mesorhaga was broken in dissection and could not be studied. The labium of Melanderia (Fig. 159) has already been described.

Pseudotracheae.—There are two kinds of pseudotracheae present in the labella of this family—those with ribbon-like panels and those with sclerotized panels. Becher (1882, p. 148) first termed these pseudotracheae "Reibleisten," which I have translated "grinding panels." The panels radiate from a small sclerotized area and end pointedly in the membrane. There is a central groove in each ribbon-like panel.

Five ribbon-like panels are found in Condylostylus (Fig. 160), and six ribbon-like panels occur in Laxina (Fig. 161), Xanthochlorus (Fig. 162), Sciapus (Fig. 163), Thrypticus (Fig. 164), Medeterus (Fig. 165), and Rhaphium (Fig. 166).

In Laxina (Fig. 161) sense organs are present between panels 2 and 3, 4 and 5, 5 and 6. Xanthochlorus (Fig. 162) has six tubulous pseudotracheae, which end rather bluntly in the membrane. The ribbons have sense organs on their apical ends. Sense organs also occur near the base of panels 1, 2, 4, 5, and 6. The central grooves of the panels are similar to Sciapus. In Medeterus (Fig. 165) the ribbons of the pseudotracheae are also tubulous, with sense pegs at the apical end of each panel. Sense organs are present between panels 1 and 2, 3 and 4, 5 and 6. The central groove of each panel is almost closed, and its edges are asperous. Sciapus (Fig. 163) has pseudotracheae almost like Xanthochlorus, but the sense organs at the proximal ends are between panels 2 and 3, 4 and 5. The central groove is very wide in some parts of the ribbons. The sclerotized area from which the panels arise is longer and wider than in Thrypticus.

The pseudotracheae with sclerotized panels are always six in number but vary in three ways: some genera (Figs. 167 and 168) are irregularly sclerotized; one genus (Fig. 169) has unpaired sclerotized areas; most others (Figs. 170 to 189) have paired (geminate), sclerotized, subrectangular areas.

Irregular sclerotized wrinklings, as well as sclerotized sub-rectangular areas, are found in the panels of the pseudotracheae of Hypocharassus

(Fig. 167) and Diostracus (Fig. 168). In Hypocharassus the sense organs occur medially between the panels and at the distal end of each panel. Diostracus has institia at the caudal margin of each panel and has sense organs at both proximal and distal ends.

Gymnopternus (Fig. 169) is the only genus that has the six panels arranged in pairs, with four unpaired, sclerotized, sub-rectangular areas in each panel.

Pseudotracheae that consist of six panels with geminate, sub-rectangular, sclerotized prominences in each panel occur in Thinophilus (Fig. 170), Millardia (Fig. 171), Hydrophorus (Fig. 172), Campsicnemus (Fig. 174), Chrysotus (Fig. 175), Diaphorus (Fig. 176), Neurigona (Fig. 177), Plagioneurus (Fig. 178), Peloropeodes (Fig. 179) and Syntormon (Fig. 180). Aphrosylus (Fig. 173) has only five panels of this kind, and its sixth panel is ribbon-like and unsclerotized. Its sense organs are at the proximal ends of panels 1, 2, 3, 4, and 5, and one long bristle-like sense hair occurs at the distal end of each panel.

Thinophilus (Fig. 170) has only a small geminately sclerotized area in each panel. There are sense pegs on the proximal ends of panels 3, 5, and 6. In Millardia (Fig. 171) the six panels have large solidly sclerotized areas at their proximal ends, followed by geminately sub-rectangular areas, which decrease in size towards the distal end. The proximal sense organs are on panels 1 and 3, and each of the six panels has a distal sense organ. Hydrophorus (Fig. 172) has an arrangement of pseudotracheae similar to Millardia, but the proximal sense organs are between panels 2 and 3, 4 and 5. The last panel of the pseudotracheae of Campsicnemus (Fig. 174) has a small unsclerotized area at its distal tip. The proximal sense organs are between panels 2 and 3, 4 and 5, 5 and 6. There is also a sense organ at the distal end of each panel. Chrysotus (Fig. 175) has six long narrow panels with paired oval areas in each. The proximal sense organs are between panels 1 and 2, 3 and 4. Each panel has a distal sense organ as in the preceding genera of this group. The panels in Diaphorus (Fig. 176) are similar to the panels of Chrysotus, but there is also a proximal sense organ between panels 5 and 6. Neurigona (Fig. 177) has a sense peg on the base of panels 1, 3, and 5 and also near the distal end of each panel. The panels in Plagioneurus (Fig. 178) are similar to those of Chrysotus and Neurigona, but the proximal sense pegs are between panels 1 and 2, 2 and 3. Peloropeodes (Fig. 179) has pseudotracheae similar to Plagioneurus, but the panels are much longer and there are five basal sense organs. The panels of Syntormon (Fig. 180) are somewhat curved at the distal ends, and the proximal sense organs lie between panels 2 and 3, 4 and 5, 5 and 6.

The following genera have geminately sclerotized sub-rectangular areas also but differ from the former group in the location of the sense

organs which are present at the distal end only: Sympycnus (Fig. 181), Liancalus (Fig. 182), Pelastoneurus (Fig. 183), Tachytrechus (Fig. 184), Scellus (Fig. 185), Dolichopus (Fig. 186), and Hygroceleuthus (Fig. 187).

The pseudotracheae of Teuchophorus (Fig. 188) and Argyra (Fig. 189) have no sense organs at either proximal or distal ends, but the panels have geminate sub-rectangular prominences as in the preceding group. Melanderia has no pseudotracheae, but an interdental armature occurs on the membrane surrounding each labellum (Fig. 190, *m*).

RELATIONSHIP OF THE GENERA BASED ON THE PRESENT STUDY

THE SIMILARITY in the shape and size, as well as the comparison of the structural characteristics found in the epipharyngeal armature and the pseudotracheae, in the different genera of the Dolichopodidae studied, have led to the following generic combinations. The hypopharyngeal characteristic was not considered in this classification because the transition of the hypopharynx from one shape to the other is so gradual that it is rather difficult to determine to which group each hypopharynx belongs. These groups are arranged in a series, from what I believe to be the most primitive to that which is most highly specialized as determined especially by the labrum and labial panels.

GROUP I.—Labrum elongated; two very short prongs; six panels geminately sclerotized:
        Diaphorus (Figs. 65 and 176)
        Chrysotus (Figs. 66 and 175)

GROUP II.—Labrum not elongated; two prongs; six panels geminately sclerotized:
        Aphrosylus (Figs. 71 and 173)
        Neurigona (Figs. 68 and 177)
        Millardia (Figs. 73 and 171)
        Scellus (Figs. 72 and 185)

GROUP III.—Labrum not elongated; two prongs; six panels irregularly sclerotized:
        Diostracus (Figs. 75 and 168)

GROUP IV.—Labrum not elongated; two prongs; six panels ribbon-like and not geminately sclerotized:
        Medeterus (Figs. 69 and 165)
        Thrypticus (Figs. 70 and 164)
        Rhaphium (Figs. 67 and 166)
        Xanthochlorus (Figs. 74 and 162)

GROUP V.—Labrum not elongated; four prongs connected; five panels ribbon-like and not geminately sclerotized:
Condylostylus (Figs. 77 and 160)

GROUP VI.—Labrum not elongated; four prongs connected; six panels ribbon-like and not geminately sclerotized:
Laxina (Figs. 76 and 161)
Sciapus (Figs. 78 and 163)
Mesorhaga (Fig. 79)

GROUP VII.—Labrum not elongated; four prongs connected; six panels geminately sclerotized:
Thinophilus (Figs. 80 and 170)

GROUP VIII.—Labrum not elongated; four prongs disconnected; six panels geminately and irregularly sclerotized:
Hypocharassus (Figs. 81 and 167)

GROUP IX.—Labrum not elongated; four prongs disconnected; no panels:
Melanderia (Fig. 82)

GROUP X.—Labrum plate-like; four prongs connected; six panels geminately sclerotized:
Argyra (Figs. 86 and 189)
Campsicnemus (Figs. 84 and 174)
Hydrophorus (Figs. 83 and 172)
Liancalus (Figs. 85 and 182)
Peloropeodes (Figs. 87 and 179)
Teuchophorus (Figs. 88 and 188)

GROUP XI.—Labrum plate-like; two prongs; six panels with sclerotizations unpaired:
Gymnopternus (Figs. 94 and 169)

GROUP XII.—Labrum plate-like; two prongs; six panels geminately sclerotized:
Dolichopus (Figs. 96 and 186)
Hygroceleuthus (Figs. 95 and 187)
Plagioneurus (Figs. 90 and 178)
Pelastoneurus (Figs. 92 and 123)
Syntormon (Figs. 91 and 180)
Sympycnus (Figs. 93 and 181)
Tachytrechus (Figs. 89 and 184)

Undoubtedly, Becker (1922) did not consider the mouth parts in his classification of subfamilies, for we find genera with the most striking structural differences grouped together. For instance the subfamily Hydrophorinae contains the following: Hydrophorus (Figs. 83 and 172), which belongs in my Group X; Scellus (Figs. 72 and 185) in Group II;

Thinophilus (Figs. 80 and 170) in Group VII; Diostracus (Figs. 75 and 168) in Group III; and Hypocharassus (Figs. 81 and 167) in Group VIII. Becker's subfamilies Campsicneminae, Chrysosomatinae, and Rhaphiinae also have several outstanding examples of generic groupings with great differentiation in the mouth parts.

SUMMARY

This study deals with the modifications and relationships of the mouth parts of thirty-two representative genera of the dipterous family Dolichopodidae. The family characteristics, habitats, and food habits of these flies are considered in order to understand more fully the mouth structures. The form and structure of the mouth parts of the thirty-two genera are illustrated by 193 drawings. It is evident from a review of the literature that previous investigators, with the exception of Langhoffer, have not observed the remarkable degree of generic variability in the mouth parts of this family and have not appreciated the value of the mouth parts from a taxonomic standpoint.

After a consideration of the various striking structural differences of the trophi in the different genera of Dolichopodidae, it is apparent to the writer that the structure of the mouth parts is of real importance in a grouping of the genera into subfamilies. On the basis of this study, the writer recognizes twelve groups of genera, including intermediate and transitional groups not observed by Langhoffer, who made the only previous study of these organs. These twelve groups may be considered as subfamilies although not so named here.

It is apparent in this work that some of the generic groupings of both Aldrich (1905) and Becker (1922), which are based on other characters, correspond with those of the writer. For instance, both authors have grouped Diaphorus and Chrysotus together, also Medeterus and Thrypticus. Other groupings of these investigators, however, do not correspond to those of the writer. This is perhaps due to the fact that neither considered the mouth parts in his classification.

In the present generic groupings the labrum, the epipharyngeal armature, and the pseudotracheae are the only mouth parts considered. These structures seem to be the most important so far as relationships between the genera are concerned. They are comparatively conspicuous, and their structural differences are so pronounced that anyone can easily recognize their differences and similarities. The hypopharynx was not considered in the grouping, because a study of it shows that there is a gradual transition in form from a simple lanceolate type to a complex pentagonal type. It has not been possible, therefore, to place each type of hypopharynx in its proper group.

In the generic arrangement a consideration of the above characters necessitated a change in the groupings of Aldrich and Becker. Regardless of other external characteristics, the writer has grouped the genera on the basis of the mouth parts in sequence from what is considered the most primitive type, as found in Group I, with the labrum elongated and two very short prongs, to that which is found in Group XII, with a plate-like labrum and two well-developed epipharyngeal prongs.

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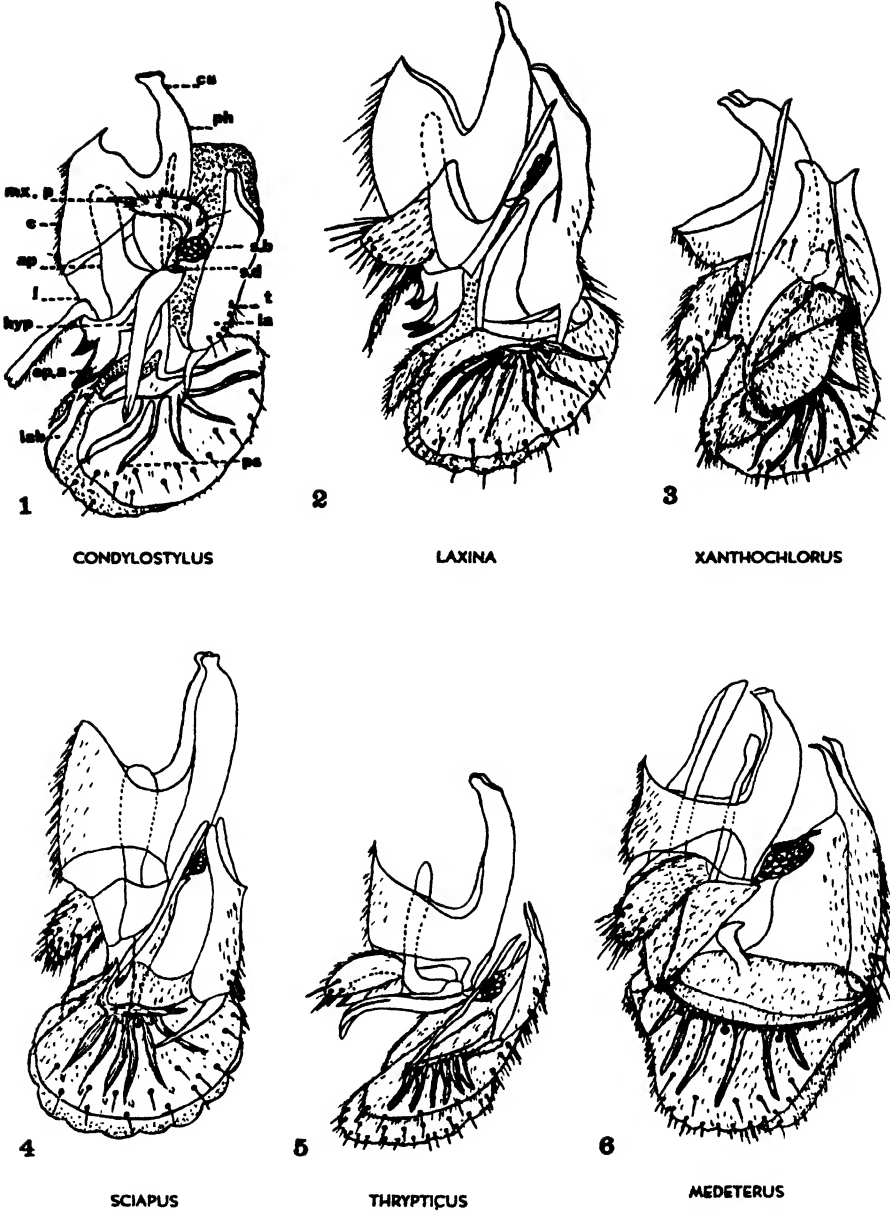   1907. Notes on the habits of *Scellus virago* Ald. Ent. News, 18:136-138.

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ABBREVIATIONS USED IN PLATES

ap........apodeme
c.........clypeus
cu........cornu
ep.a......epipharyngeal armature
g.........glossae
hyp.......hypopharynx
l.........labrum
la........labium
lab.......labellum
l.r.......lateral rod
m........membrane
mx.p......maxillary palpus

p...........panel
ph..........pharynx
ps..........pseudotracheae
s...........sense organ
sac........sack
s.b.........salivary bulb
sc.p........sclerotized plate
s.d.........salivary duct
sh..........sense hair
sp..........sense peg
t...........theca

PLATE I

Lateral Aspect of the Complete Feeding Mechanism

Fig. 1.   *Condylostylus sipho* Say, female.
Fig. 2.   *Laxina calcarata* Lw., male.
Fig. 3.   *Xanthochlorus helvinus* Lw., female.
Fig. 4.   *Sciapus scintillans* Lw., female.
Fig. 5.   *Thrypticus willistoni* Wheel., female.
Fig. 6.   *Medeterus aldrichi* Wheel., male.
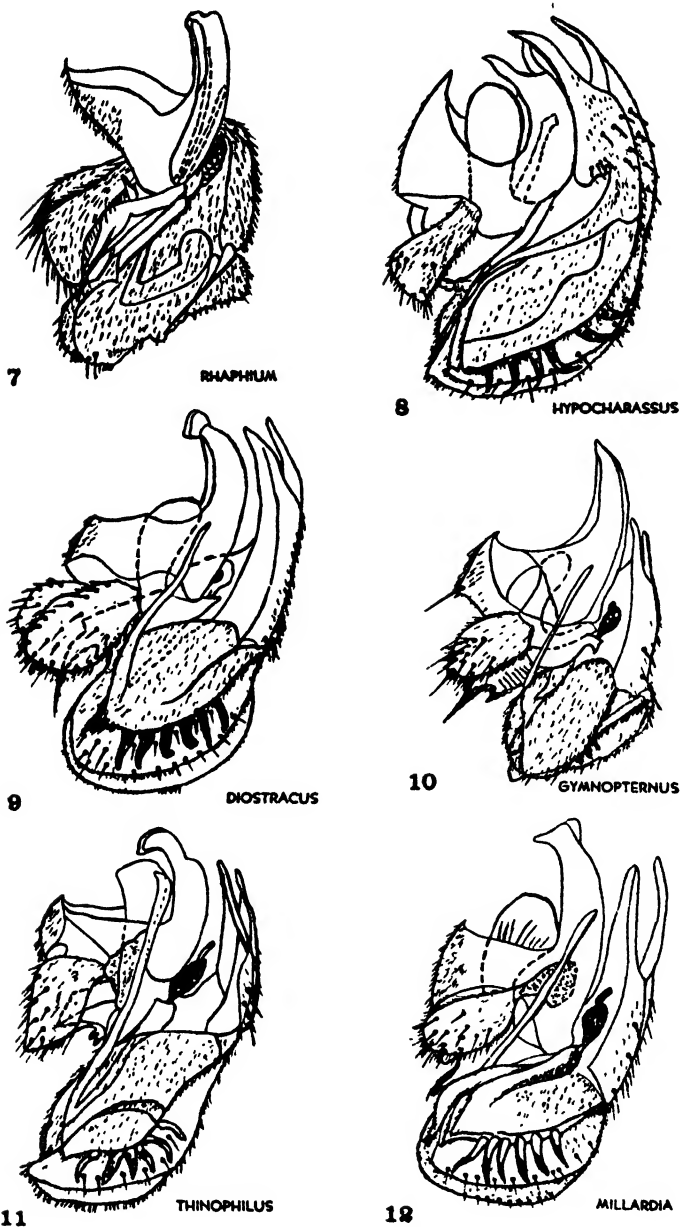
PLATE II

Lateral Aspect of Complete Feeding Mechanism

FIG. 7. *Rhaphium effilatus* Wheel., male.
FIG. 8. *Hypocharassus pruinosus* Wheel., female.
FIG. 9. *Diostracus prasinus* Lw., female.
FIG. 10. *Gymnopternus barbatulus* Lw., male.
FIG. 11. *Thinophilus ochrifacies* V. D., male.
FIG. 12. *Millardia intentus* Aldr., female.
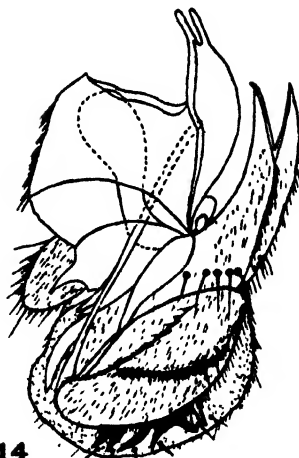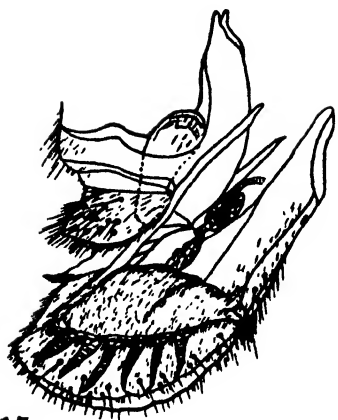
PLATE III

Lateral Aspect of Complete Feeding Mechanism

Fig. 13. *Hydrophorus sodalis* Wheel., female.
Fig. 14. *Aphrosylus praedator* Wheel., female.
Fig. 15. *Campsicnemus nigripes* V. D., male.
Fig. 16. *Chrysotus choricus* Wheel., male.
Fig. 17. *Diaphorus leucostomus* Lw., male.
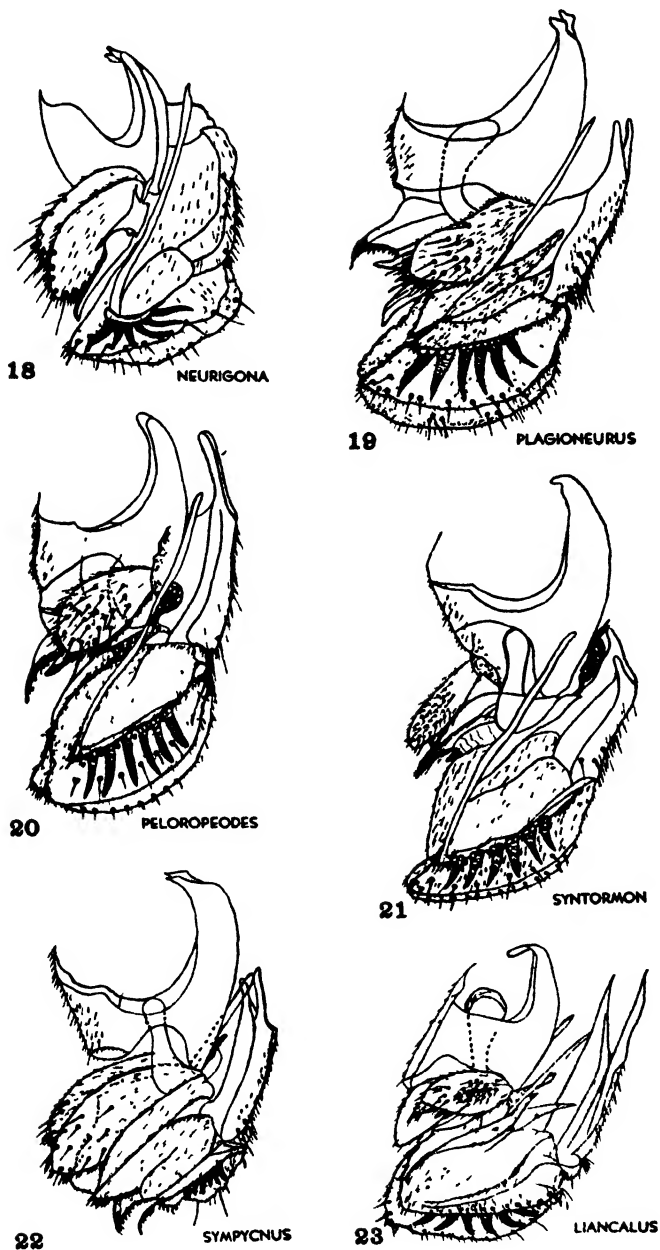
PLATE IV

Lateral Aspect of Complete Feeding Mechanism

Fig. 18. *Neurigona carbonifer* Lw., female.
Fig. 19. *Plagioneurus univittatus* Lw., female.
Fig. 20. *Peloropeodes acuticornis* V. D., male.
Fig. 21. *Syntormon cinereiventris* Lw., male.
Fig. 22. *Sympycnus lineatus* Lw., male.
Fig. 23. *Liancalus similis* Aldr., male.
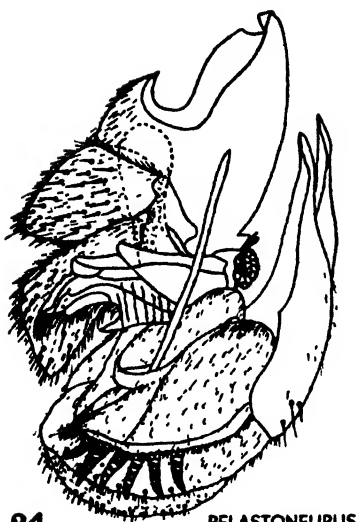
24 PELASTONEURUS

25 TACHYTRECHUS

26 SCELLUS

27 DOLICHOPUS

PLATE V

Lateral Aspect of Complete Feeding Mechanism

FIG. 24. *Pelastoneurus vagans* Lw., female.
FIG. 25. *Tachytrechus angustipennis* Lw., female.
FIG. 26. *Scellus filiferus* Lw., female.
FIG. 27. *Dolichopus ramifer* Lw., female.
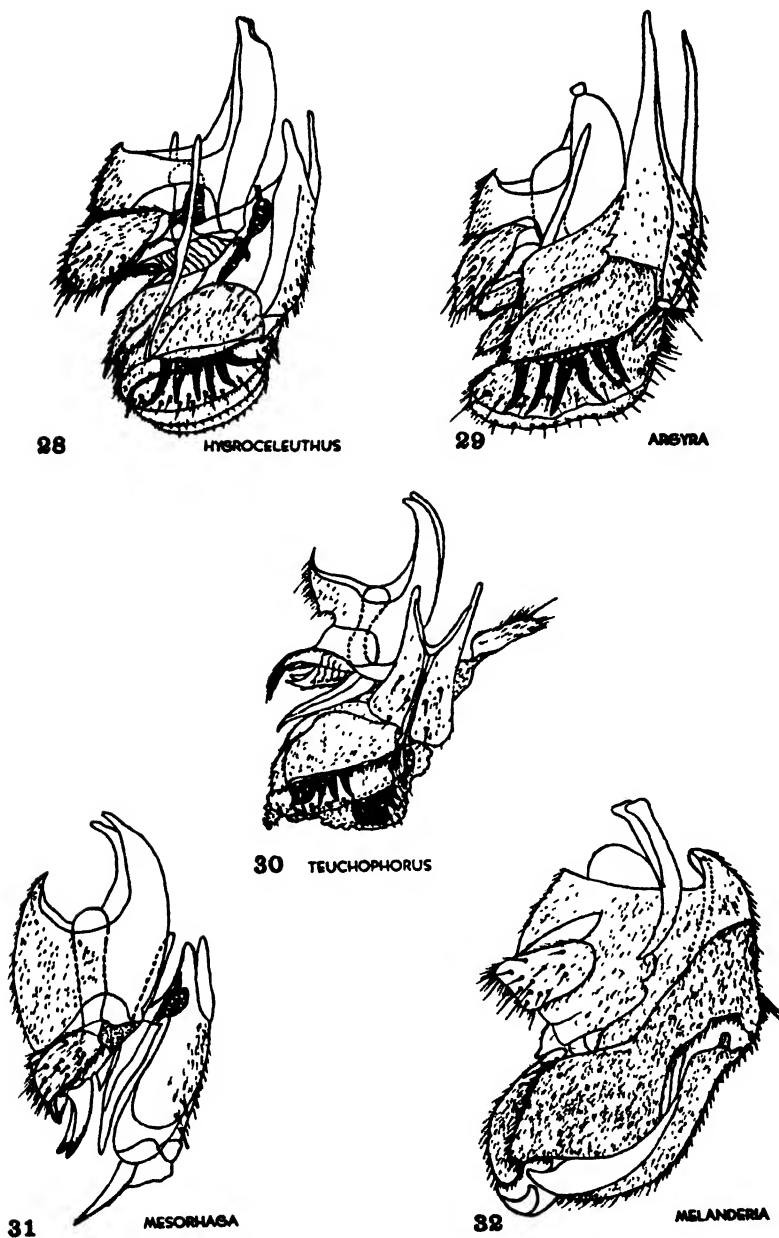
PLATE VI

Lateral Aspect of Complete Feeding Mechanism

Fɪɢ. 28. *Hygroceleuthus consanguineus* Wheel., male.
Fɪɢ. 29. *Argyra albicans* Lw., female.
Fɪɢ. 30. *Teuchophorus spinigerellus* Zett., female.
Fɪɢ. 31. *Mesorhaga* sp., female.
Fɪɢ. 32. *Melanderia mandibulata* Aldr., male.
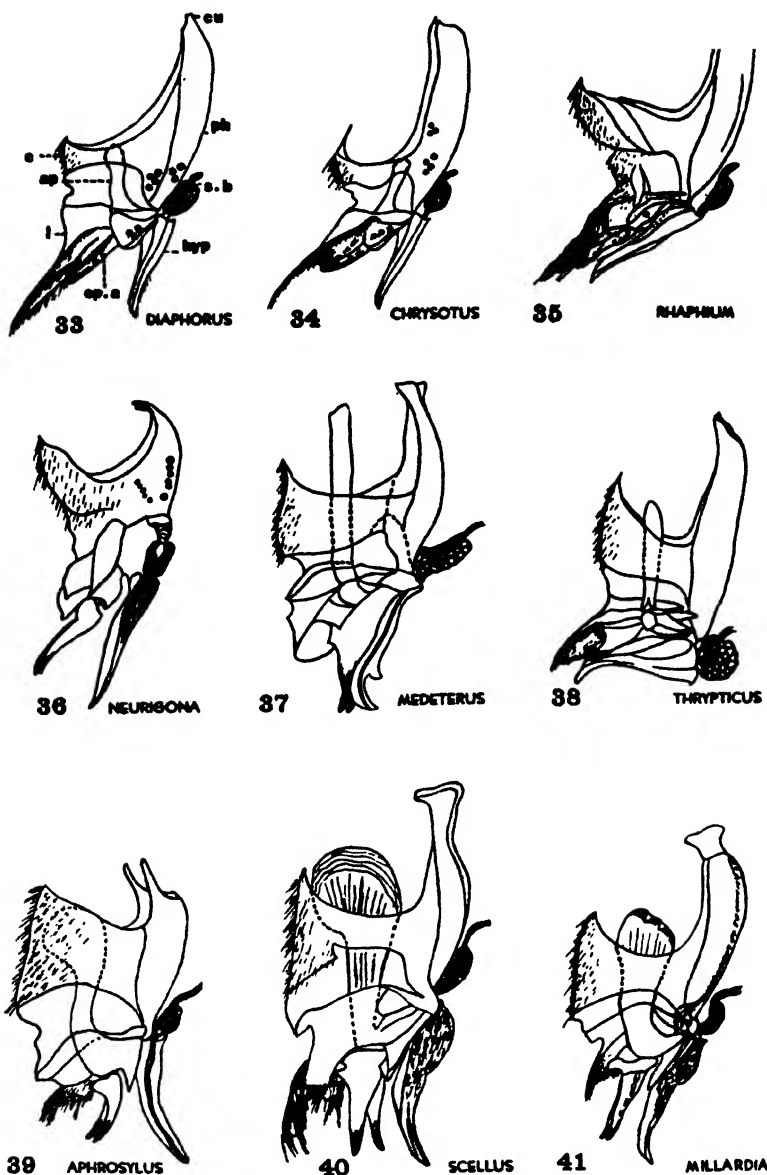
PLATE VII

Lateral Aspect of Clypeolabral-Pharyngeal Region

FIG. 33.   *Diaphorus leucostomus* Lw., male.
FIG. 34.   *Chrysotus choricus* Wheel., male.
FIG. 35.   *Rhaphium effilatus* Wheel., male.
FIG. 36.   *Neurigona carbonifer* Lw., female.
FIG. 37.   *Medeterus aldrichi* Wheel., male.
FIG. 38.   *Thrypticus willistoni* Wheel., male.
FIG. 39.   *Aphrosylus praedator* Wheel., female.
FIG. 40.   *Scellus filiferus* Lw., female.
FIG. 41.   *Millardia intentus* Aldr., female.
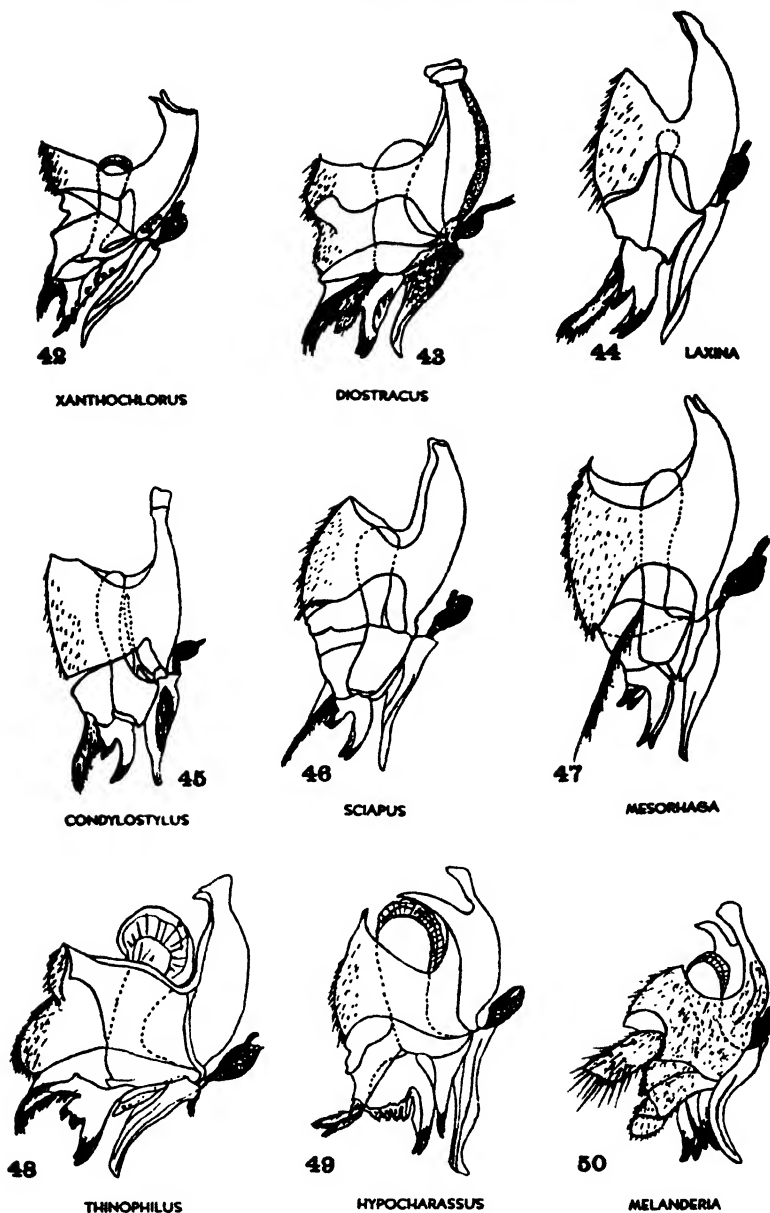
PLATE VIII

Lateral Aspect of Clypeolabral-Pharyngeal Region

FIG. 42. *Xanthochlorus helvinus* Lw., female.
FIG. 43. *Diostracus prasinus* Lw., female.
FIG. 44. *Laxina calcarata* Lw., male.
FIG. 45. *Condylostylus sipho* Say, female.
FIG. 46. *Sciapus scintillans* Lw., female.
FIG. 47. *Mesorhaga* sp., female.
FIG. 48. *Thinophilus ochrifacies* V. D., male.
FIG. 49. *Hypocharassus pruinosus* Wheel., female.
FIG. 50. *Melanderia mandibulata* Aldr., male.
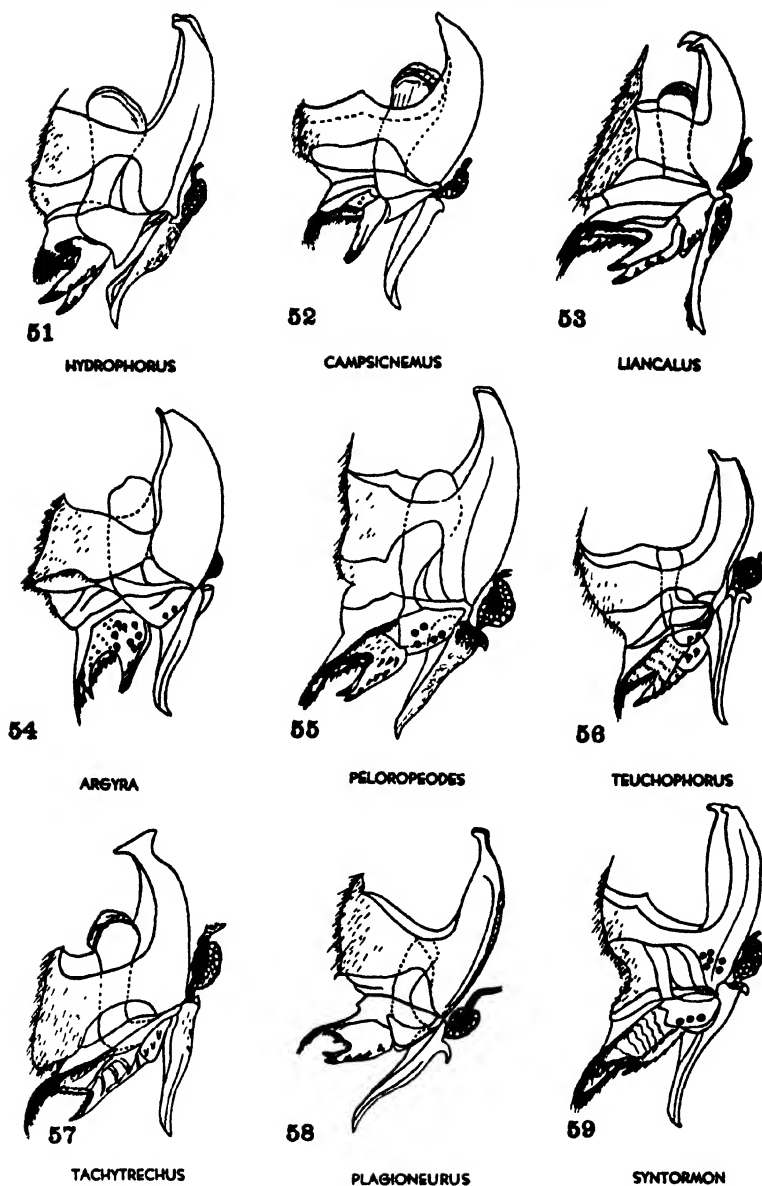
PLATE IX

Lateral Aspect of Clypeolabral-Pharyngeal Region

FIG. 51. *Hydrophorus sodalis* Wheel., female.
FIG. 52. *Campsicnemus nigripes* V. D., male.
FIG. 53. *Liancalus similis* Aldr., male.
FIG. 54. *Argyra albicans* Lw., female.
FIG. 55. *Peloropeodes acuticornis* V. D., male.
FIG. 56. *Teuchophorus spinigerellus* Zett., female.
FIG. 57. *Tachytrechus angustipennis* Lw., female.
FIG. 58. *Plagioneurus univittatus* Lw., female.
FIG. 59. *Syntormon cinereiventris* Lw., male.
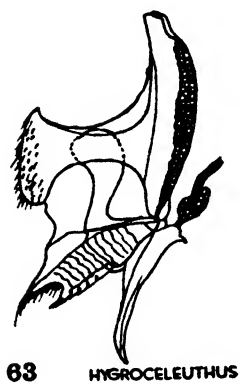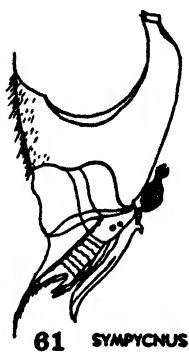
PLATE X

Lateral Aspect of Clypeolabral-Pharyngeal Region

Fig. 60. *Pelastoneurus vagans* Lw., female.
Fig. 61. *Sympycnus lineatus* Lw., male.
Fig. 62. *Gymnopternus barbatulus* Lw., male.
Fig. 63. *Hygroceleuthus consanguineus* Wheel., male.
Fig. 64. *Dolichopus ramifer* Lw., female.
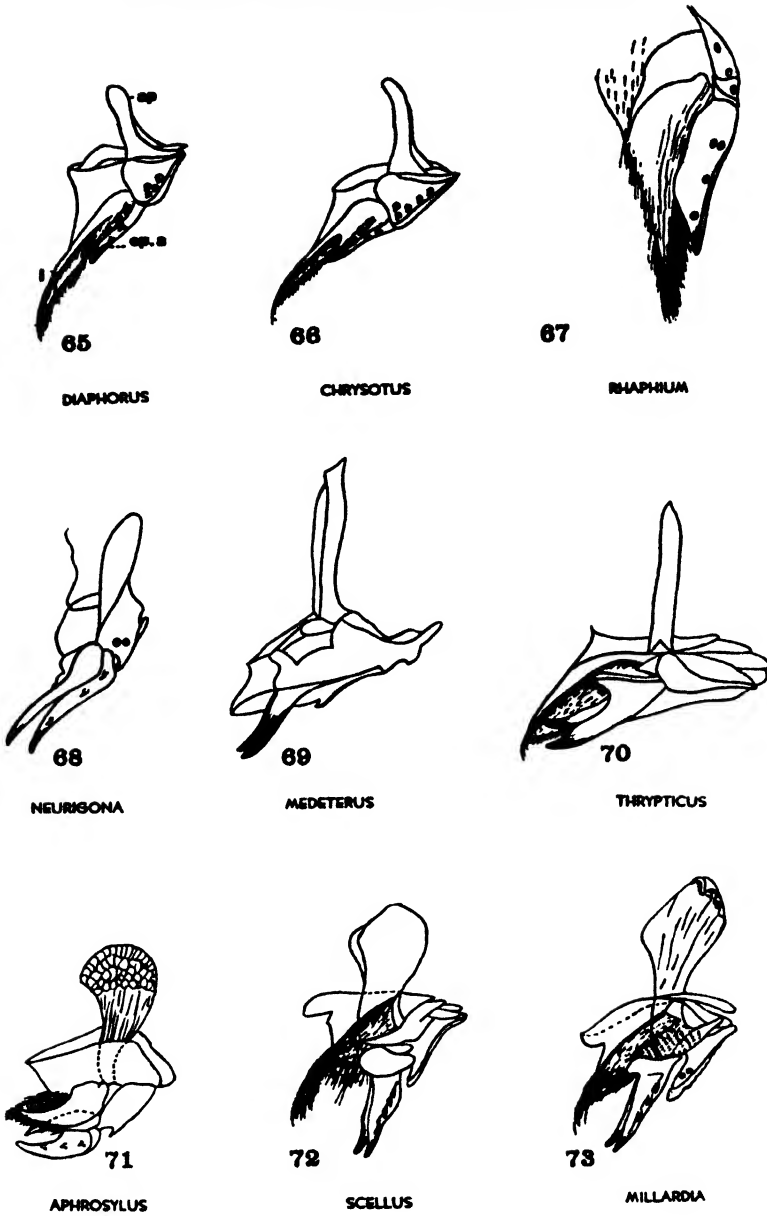
PLATE XI

Lateral Aspect of Epipharyngeal Armature

Fig. 65. *Diaphorus leucostomus* Lw., male.
Fig. 66. *Chrysotus choricus* Wheel., male.
Fig. 67. *Rhaphium effilatus* Wheel., male.
Fig. 68. *Neurigona carbonifer* Lw., female.
Fig. 69. *Medeterus aldrichi* Wheel., male.
Fig. 70. *Thrypticus willistoni* Wheel., male.
Fig. 71. *Aphrosylus praedator* Wheel., female.
Fig. 72. *Scellus filiferus* Lw., female.
Fig. 73. *Millardia intentus* Aldr., female.
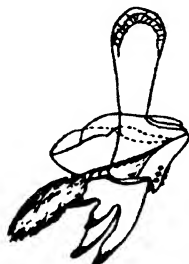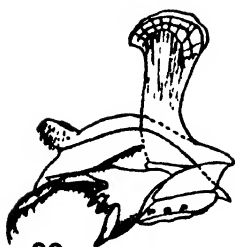
PLATE XII

Lateral Aspect of Epipharyngeal Armature

Fig. 74. *Xanthochlorus helvinus* Lw., female.
Fig. 75. *Diostracus prasinus* Lw., female.
Fig. 76. *Laxina calcarata* Lw., male.
Fig. 77. *Condylostylus sipho* Say, female.
Fig. 78. *Sciapus scintillans* Lw., female.
Fig. 79. *Mesorhaga* sp., female.
Fig. 80. *Thinophilus ochrifacies* V. D., male.
Fig. 81. *Hypocharassus pruinosus* Wheel., female.
Fig. 82. *Melanderia mandibulata* Aldr., male.
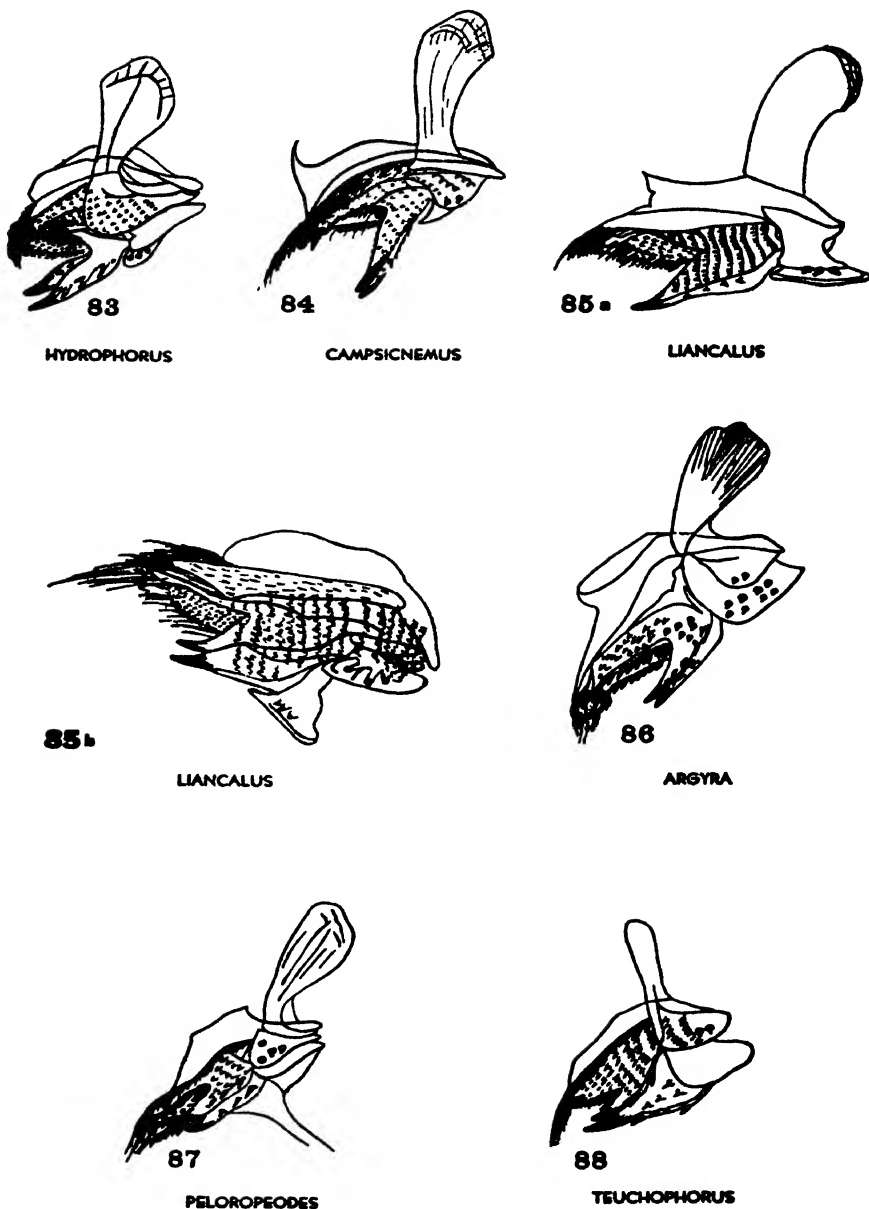
PLATE XIII

Lateral Aspect of Epipharyngeal Armature

FIG. 83. *Hydrophorus sodalis* Wheel., female.
FIG. 84. *Campsicnemus nigripes* V. D., male.
FIG. 85a. *Liancalus similis* Aldr., male.
FIG. 85b. *Liancalus similis* Aldr., male (more detailed study).
FIG. 86. *Argyra albicans* Lw., female.
FIG. 87. *Peloropeodes acuticornis* V. D., male.
FIG. 88. *Teuchophorus spinigerellus* Zett., female.
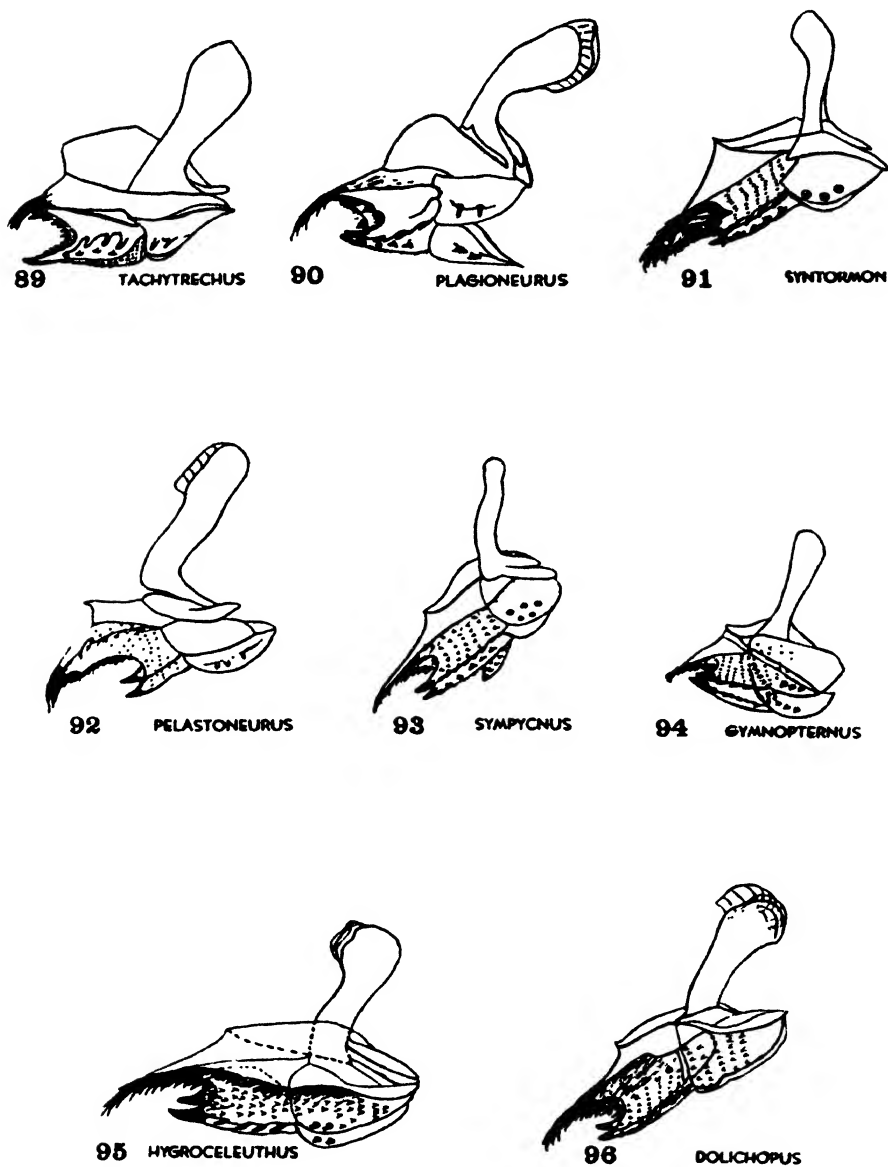
PLATE XIV

Lateral Aspect of Epipharyngeal Armature

FIG. 89. *Tachytrechus angustipennis* Lw., female.
FIG. 90. *Plagioneurus univittatus* Lw., female.
FIG. 91. *Syntormon cinereiventris* Lw., male.
FIG. 92. *Pelastoneurus vagans* Lw., female.
FIG. 93. *Sympycnus lineatus* Lw., male.
FIG. 94. *Gymnopternus barbatulus* Lw., male.
FIG. 95. *Hygroceleuthus consanguineus* Wheel., male.
FIG. 96. *Dolichopus ramifer* Lw., female.
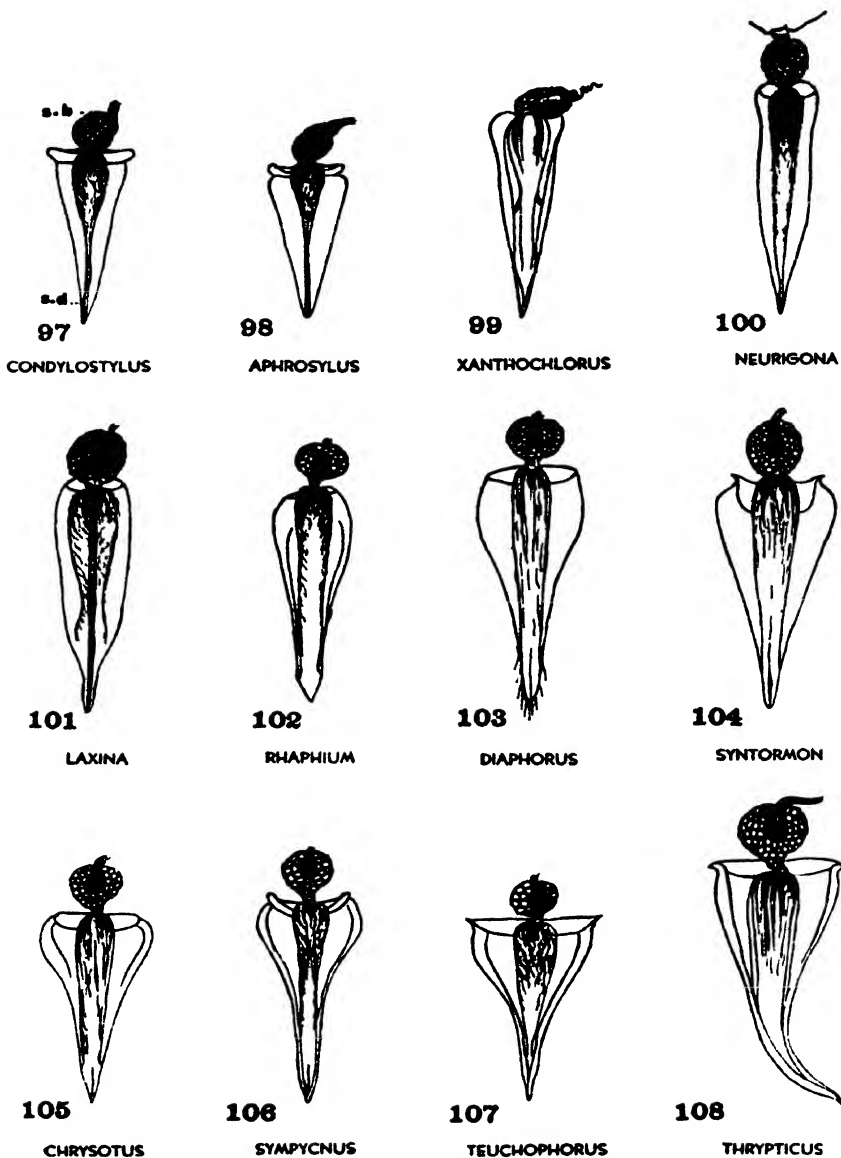
PLATE XV

Cephalic Aspect of Hypopharynx

FIG. 97.   *Condylostylus sipho* Say, female.
FIG. 98.   *Aphrosylus praedator* Wheel., female.
FIG. 99.   *Xanthochlorus helvinus* Lw., female.
FIG. 100.   *Neurigona carbonifer* Lw., female.
FIG. 101.   *Laxina calcarata* Lw., male.
FIG. 102.   *Rhaphium effilatus* Wheel., male.
FIG. 103.   *Diaphorus leucostomus* Lw., male.
FIG. 104.   *Syntormon cinereiventris* Lw., male.
FIG. 105.   *Chrysotus choricus* Wheel., male.
FIG. 106.   *Sympycnus lineatus* Lw., male.
FIG. 107.   *Teuchophorus spinigerellus* Zett., female.
FIG. 108.   *Thrypticus willistoni* Wheel., male.

109 TACHYTRECHUS
110a MEDETERUS
110b MEDETERUS
111 CAMPSICNEMUS
112 PLAGIONEURUS
113 ARGYRA
114 LIANCALUS
115 DOLICHOPUS
116 HYGROCELEUTHUS
117 PELOROPEODES
118 HYPOCHARASSUS
119 MELANDERIA
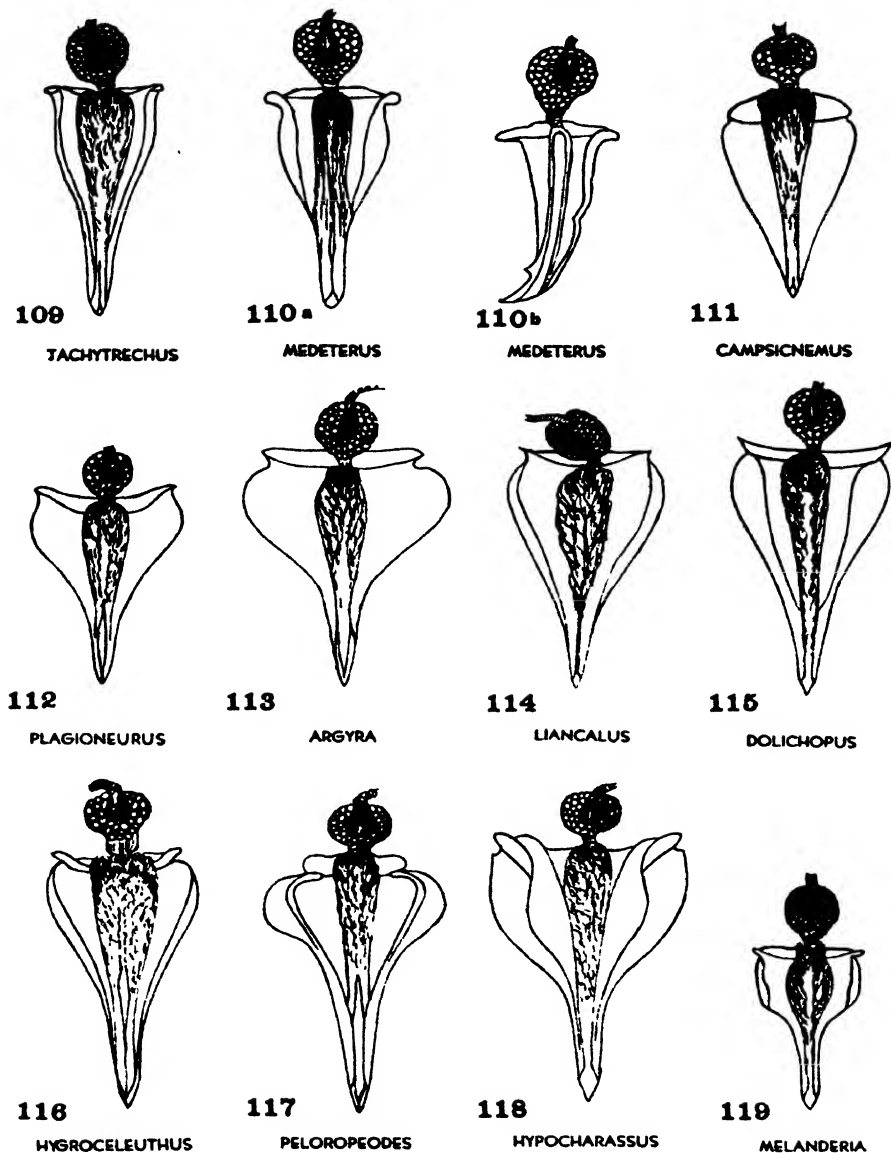
PLATE XVI

Cephalic Aspect of Hypopharynx

FIG. 109. *Tachytrechus angustipennis* Lw., female.
FIG. 110a. *Medeterus aldrichi* Wheel., male.
FIG. 110b. Lateral aspect of 110a.
FIG. 111. *Campsicnemus nigripes* V. D., male.
FIG. 112. *Plagioneurus univittatus* Lw., female.
FIG. 113. *Argyra albicans* Lw., female.
FIG. 114. *Liancalus similis* Aldr., male.
FIG. 115. *Dolichopus ramifer* Lw., female.
FIG. 116. *Hygroceleuthus consanguineus* Wheel., male.
FIG. 117. *Peloropeodes acuticornis* V. D., male.
FIG. 118. *Hypocharassus pruinosus* Wheel., female.
FIG. 119. *Melanderia mandibulata* Aldr., male.

120
THINOPHILUS

121
DIOSTRACUS

122
GYMNOPTERNUS

123
PELASTONEURUS

124
SCIAPUS

125
MESORHAGA

126
MILLARDIA

127
SCELLUS

128a
HYDROPHORUS

128b
HYDROPHORUS
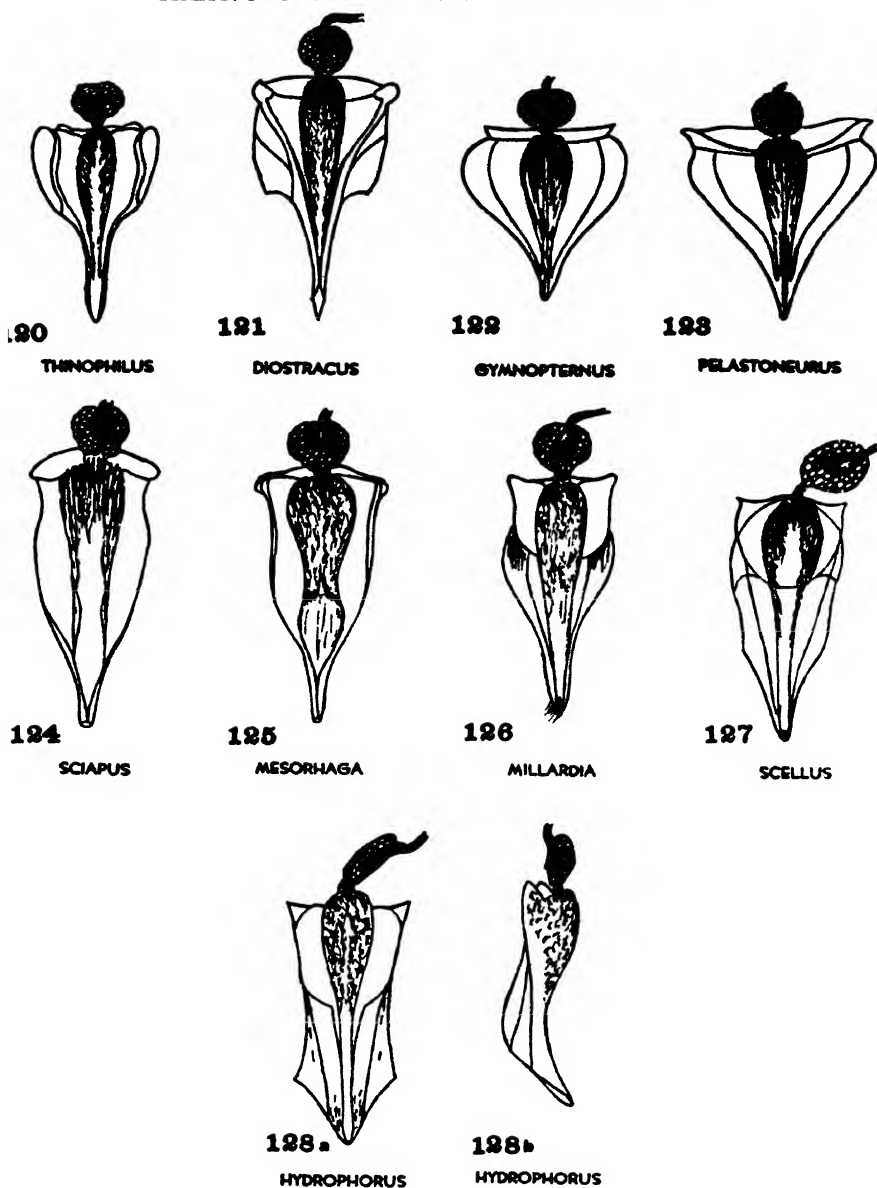
PLATE XVII

Cephalic Aspect of Hypopharynx

FIG. 120. *Thinophilus ochrifacies* V. D., male.
FIG. 121. *Diostracus prasinus* Lw., female.
FIG. 122. *Gymnopternus barbatulus* Lw., male.
FIG. 123. *Pelastoneurus vagans* Lw., female.
FIG. 124. *Sciapus scintillans* Lw., female.
FIG. 125. *Mesorhaga* sp., female.
FIG. 126. *Millardia intentus* Aldr., female.
FIG. 127. *Scellus filiferus* Lw., female.
FIG. 128a. *Hydrophorus sodalis* Wheel., female.
FIG. 128b. Lateral aspect of 128a.
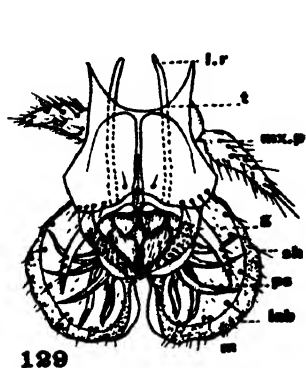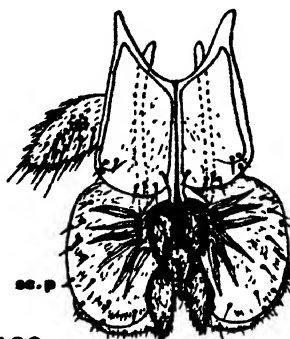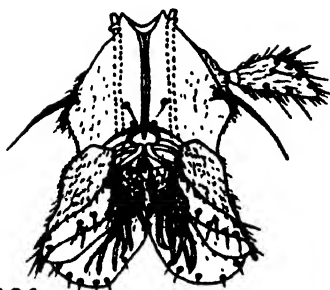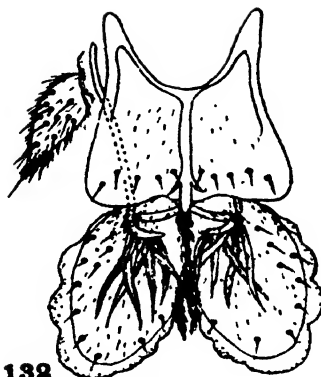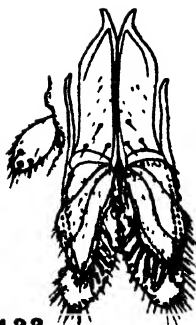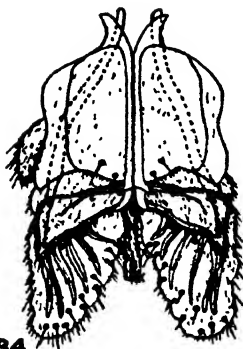
PLATE XVIII

Caudal Aspect of Labium

FIG. 129. *Condylostylus sipho* Say, female.
FIG. 130. *Laxina calcarata* Lw., male.
FIG. 131. *Xanthochlorus helvinus* Lw., female.
FIG. 132. *Sciapus scintillans* Lw., female.
FIG. 133. *Thrypticus willistoni* Wheel., male.
FIG. 134. *Medeterus aldrichi* Wheel., male.
FIG. 135. *Rhaphium effilatus* Wheel., male.
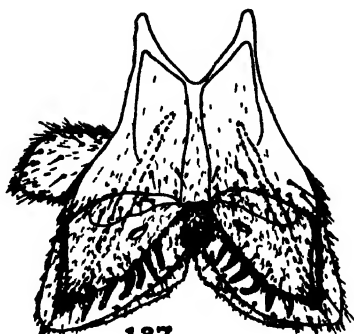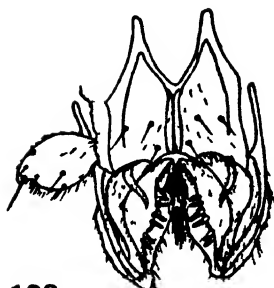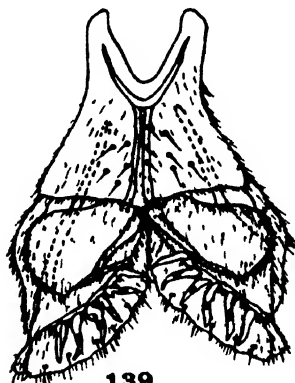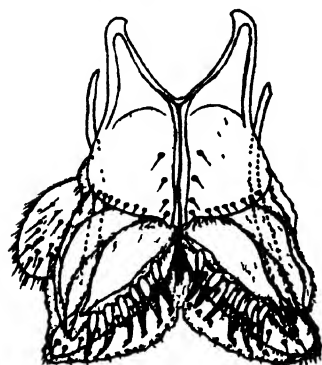
PLATE XIX

Caudal Aspect of Labium

FIG. 136.   *Hypocharassus pruinosus* Wheel, female.
FIG. 137.   *Diostracus prasinus* Lw., female.
FIG. 138.   *Gymnopternus barbatulus* Lw., male.
FIG. 139.   *Thinophilus ochrifacies* V. D., male.
FIG. 140.   *Millardia intentus* Aldr., female.
FIG. 141.   *Hydrophorus sodalis* Wheel., female.

142ᵃ APHROSYLUS

142ᵇ APHROSYLUS

143 CAMPSICNEMUS

144 CHRYSOTUS

145 DIAPHORUS

146 NEURIGONA

147 PLAGIONEURUS

148 PELOROPEODES
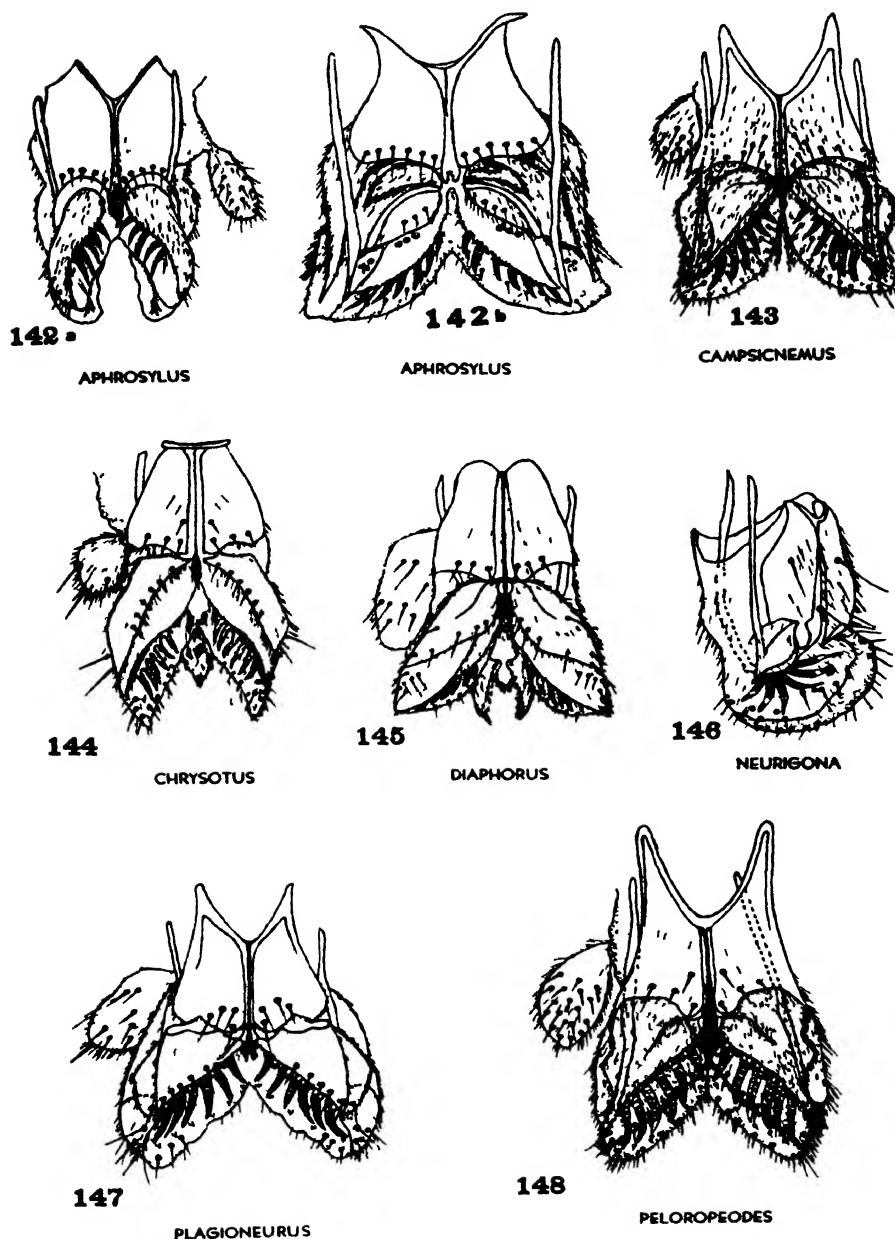
PLATE XX

Caudal Aspect of Labium

FIG. 142a. *Aphrosylus praedator* Wheel., female.
FIG. 142b. Cephalic aspect of 142a.
FIG. 143. *Campsicnemus nigripes* V. D., male.
FIG. 144. *Chrysotus choricus* Wheel., male.
FIG. 145. *Diaphorus leucostomus* Lw., male.
FIG. 146. *Neurigona carbonifer* Lw., female.
FIG. 147. *Plagioneurus univittatus* Lw., female.
FIG. 148. *Peloropeodes acuticornis* V. D., male.
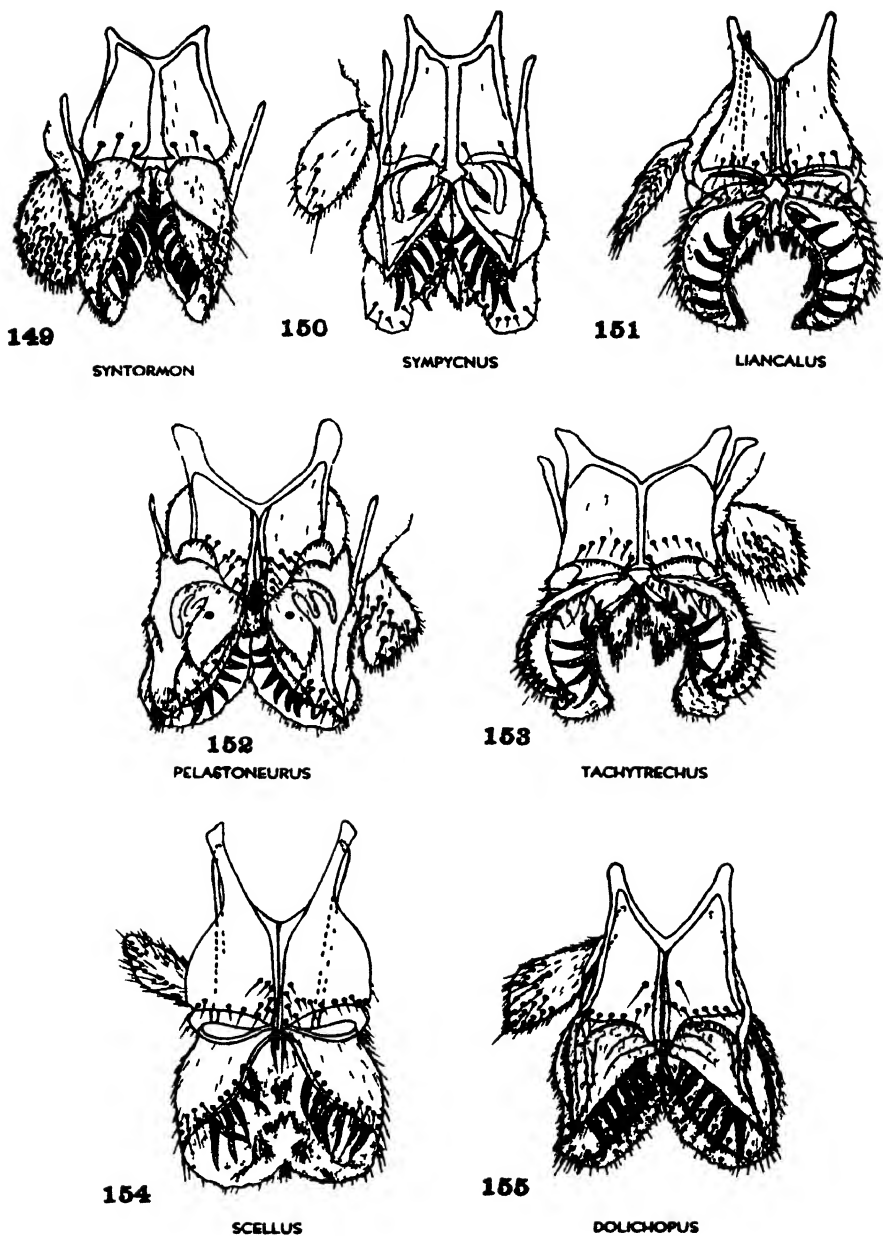
PLATE XXI

Caudal Aspect of Labium

Fig. 149   *Syntormon cinereiventris* Lw., male.
Fig. 150.   *Sympycnus lineatus* Lw., male.
Fig. 151.   *Liancalus similis* Aldr., male.
Fig. 152.   *Pelastoneurus vagans* Lw., female.
Fig. 153.   *Tachytrechus angustipennis* Lw., female.
Fig. 154.   *Scellus filiferus* Lw., female.
Fig. 155.   *Dolichopus ramifer* Lw., female.
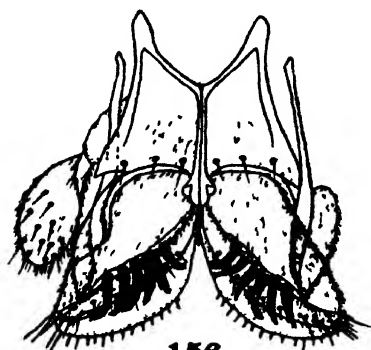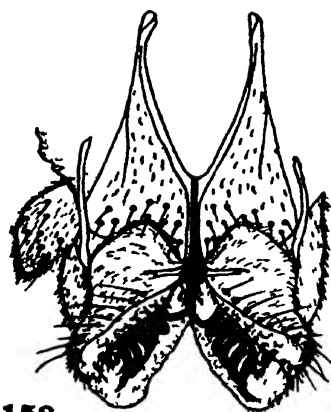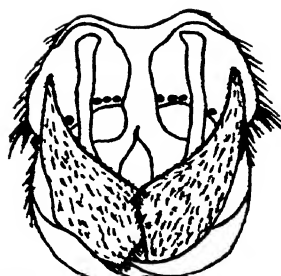
PLATE XXÍI

Caudal Aspect of Labium

Fig. 156. *Hygroceleuthus consanguineus* Wheel., male.
Fig. 157. *Teuchophorus spinigerellus* Zett., female.
Fig. 158. *Argyra albicans* Lw., female.
Fig. 159a. *Melanderia mandibulata* Aldr., male.
Fig. 159b. Cephalic aspect of 159a.
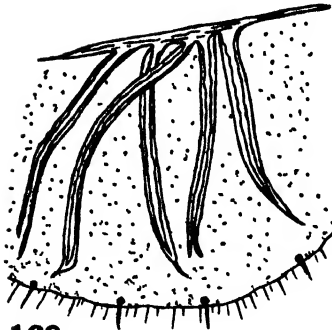
160
CONDYLOSTYLUS
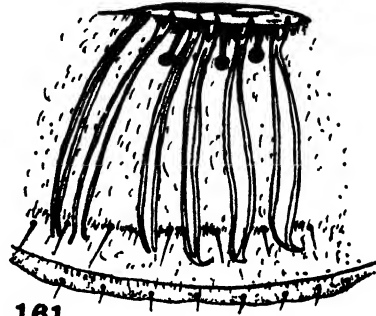
161
LAXINA
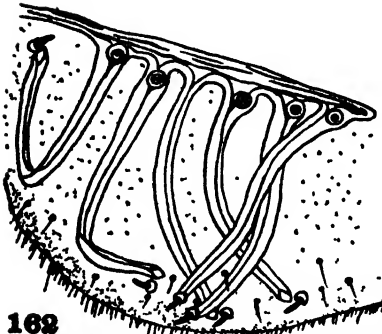
162
XANTHOCHLORUS
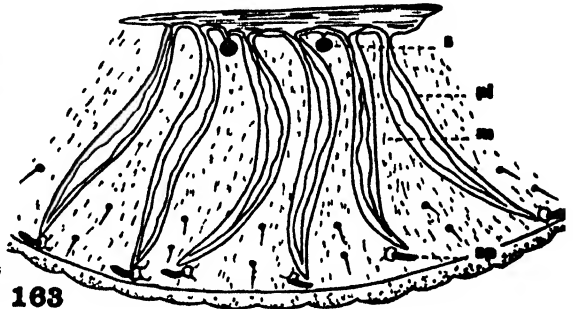
163
SCIAPUS
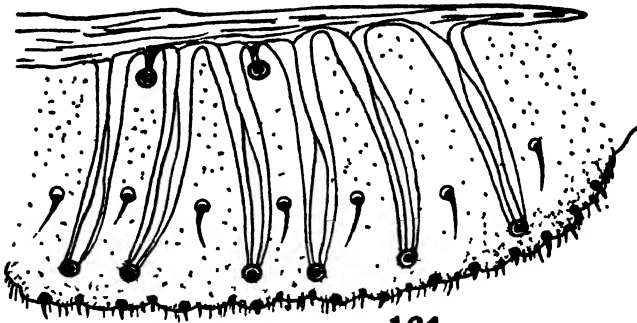
164
THRYPTICUS

PLATE XXIII
Pseudotracheae

FIG 160.   *Condylostylus sipho* Say, female.
FIG. 161.   *Laxina calcarata* Lw., male.
FIG. 162.   *Xanthochlorus helvinus* Lw., female.
FIG. 163.   *Sciapus scintillans* Lw., female.
FIG. 164.   *Thrypticus willistoni* Wheel., male.
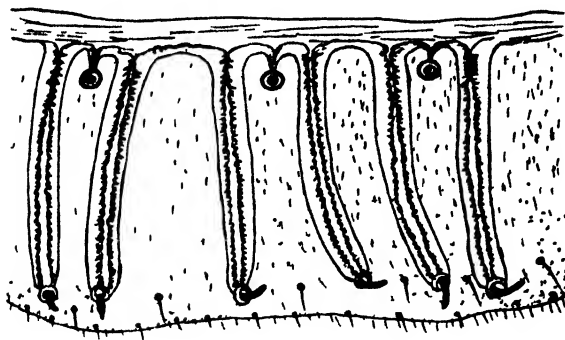
165   MEDETERUS
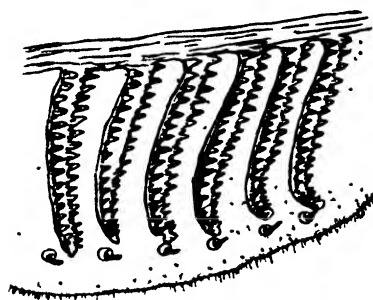
166   RHAPHIUM
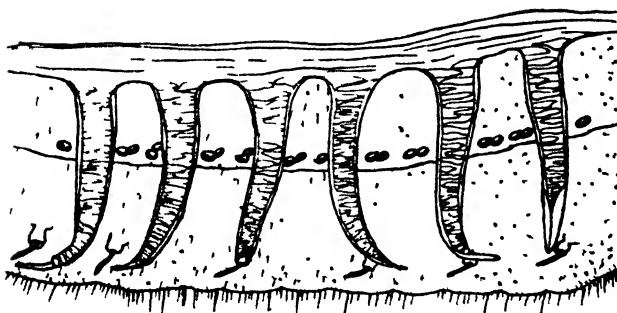
167   HYPOCHARASSUS

PLATE XXIV

Pseudotracheae

FIG. 165. *Medeterus aldrichi* Wheel., male.
FIG. 166. *Rhaphium effilatus* Wheel., male.
FIG. 167. *Hypocharassus pruinosus* Wheel., female.
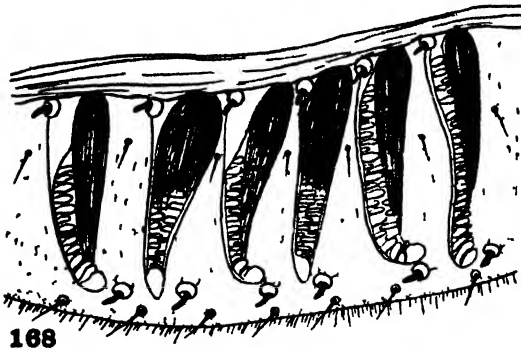
168 DIOSTRACUS
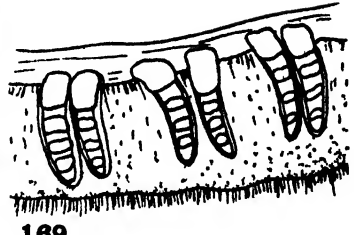
169 GYMNOPTERNUS
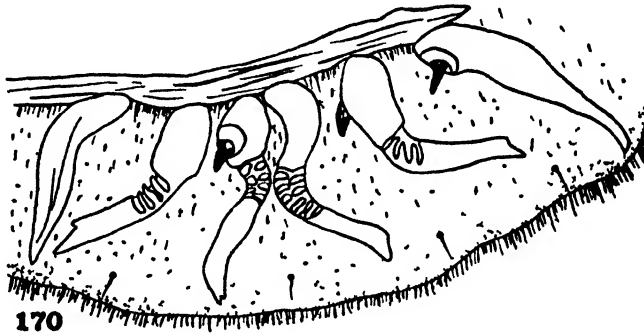
170 THINOPHILUS
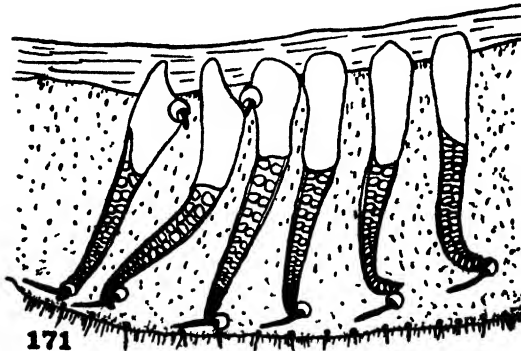
171 MILLARDIA

PLATE XXV

Pseudotracheae

Fig. 168. *Diostracus prasinus* Lw., female.
Fig 169. *Gymnopternus barbatulus* Lw., male
Fig. 170. *Thinophilus ochrifacies* V. D., male
Fig 171 *Millardia intentus* Aldr , female.
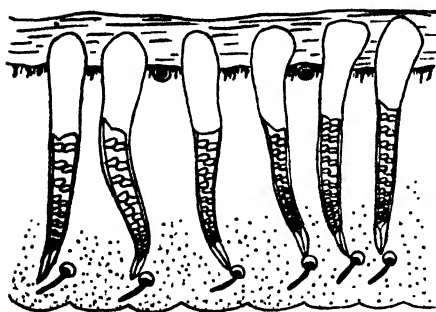
172 HYDROPHORUS
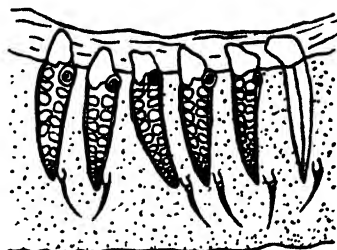
173 APHROSYLUS
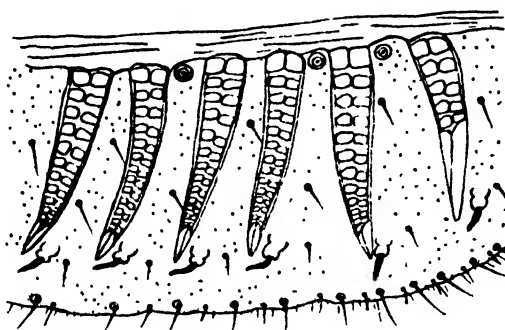
174 CAMPSICNEMUS
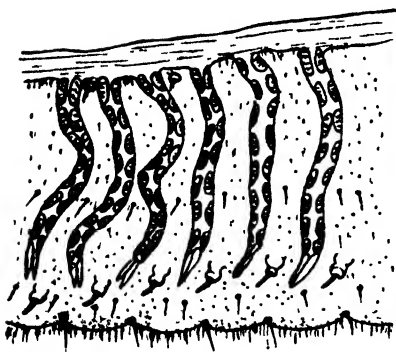
175 CHRYSOTUS
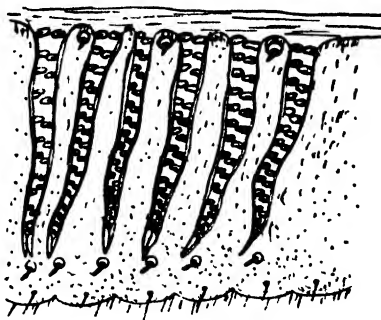
176 DIAPHORUS

PLATE XXVI
Pseudotracheae

FIG. 172. *Hydrophorus sodalis* Wheel., female.
FIG. 173. *Aphrosylus praedator* Wheel., female.
FIG. 174. *Campsicnemus nigripes* V. D., male.
FIG. 175. *Chrysotus choricus* Wheel., male.
FIG. 176. *Diaphorus leucostomus* Lw., male.
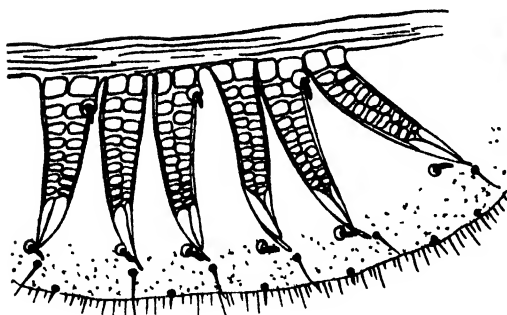
177   NEURIGONA
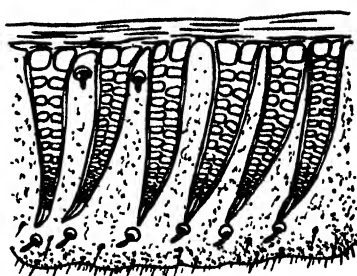
178   PLAGIONEURUS
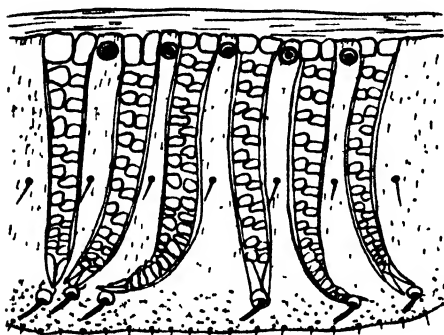
179   PELOROPEODES
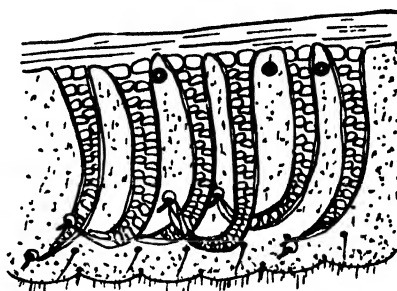
180   SYNTORMON
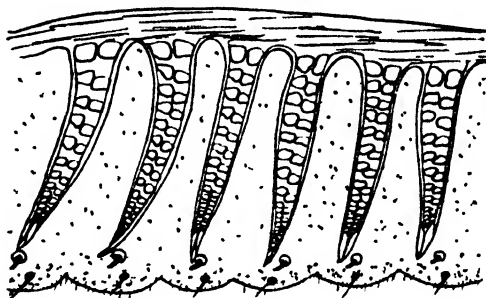
181   SYMPYCNUS

PLATE XXVII

Pseudotracheae

FIG. 177. *Neurigona carbonifer* Lw., female.
FIG. 178. *Plagioneurus univittatus* Lw., female.
FIG. 179. *Peloropeodes acuticornis* V. D., male
FIG. 180. *Syntormon cinereiventris* Lw., male.
FIG. 181. *Sympycnus lineatus* Lw., male.
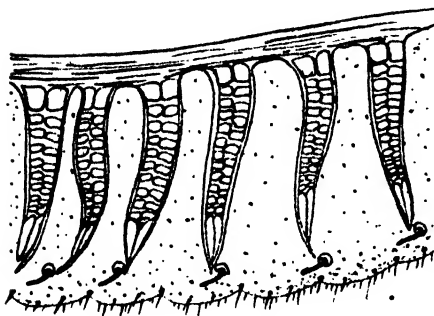
182 LIANCALUS
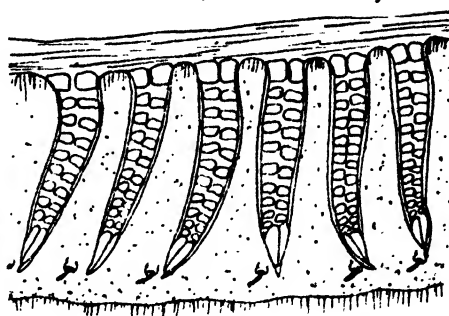
183 PELASTONEURUS
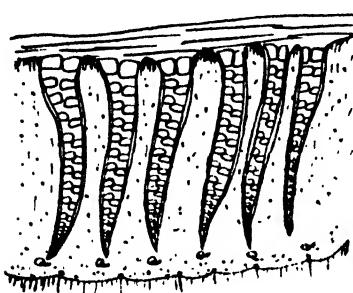
184 TACHYTRECHUS
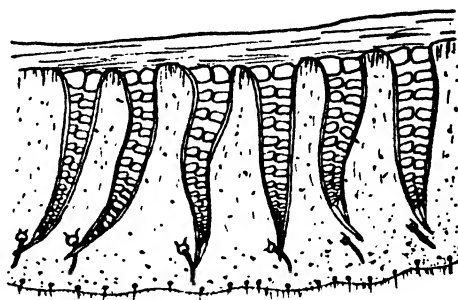
185 SCELLUS
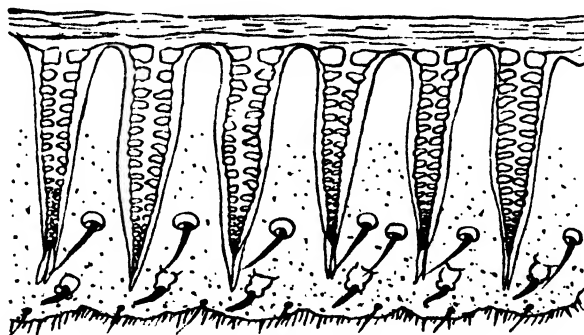
186 DOLICHOPUS

PLATE XXVIII
Pseudotracheae

FIG. 182. *Liancalus similis* Aldr., male.
FIG. 183. *Pelastoneurus vagans* Lw., female.
FIG. 184. *Tachytrechus angustipennis* Lw., female.
FIG. 185. *Scellus filiferus* Lw., female.
FIG. 186. *Dolichopus ramifer* Lw., female.
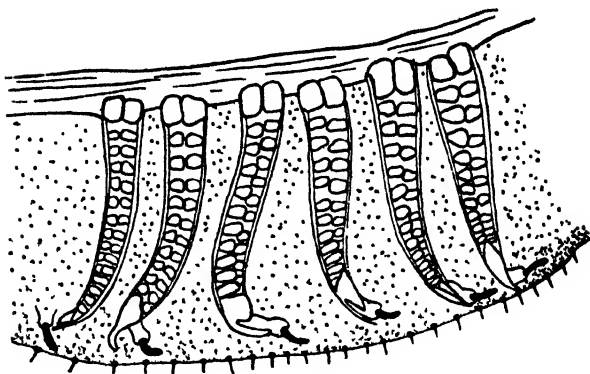
187   HYGROCELEUTHUS
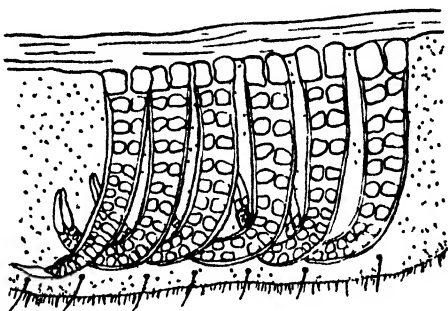
188   TEUCHOPHORUS
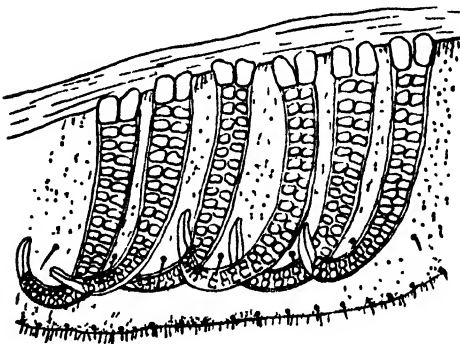
189   ARGYRA

PLATE XXIX

Pseudotracheae

FIG. 187. *Hygroceleuthus consanguineus* Wheel., male.
FIG. 188. *Teuchophorus spinigerellus* Zett., female.
FIG. 189. *Argyra albicans* Lw., female.

190

MELANDERIA

191

DOLICHOPUS   MAXILLARY PALPUS
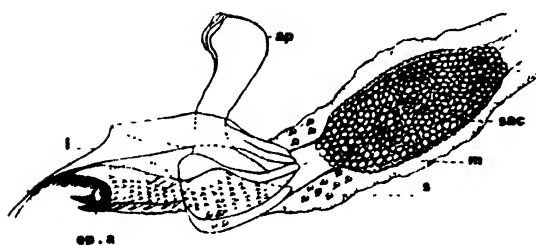
192

DOLICHOPUS   PHARYNGEAL SACK
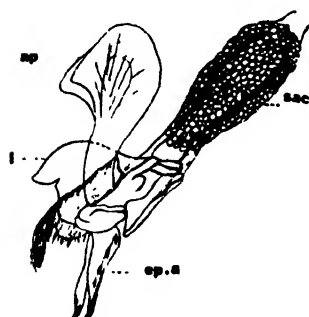
193

SCELLUS   PHARYNGEAL SACK

PLATE XXX

FIG. 190. *Melanderia mandibulata* Aldr.—Interdental armature.
FIG. 191. *Dolichopus ramifer* Lw.—Maxillary palpus.
FIG. 192. *Dolichopus ramifer* Lw.—Pharyngeal sack.
FIG. 193. *Scellus filiferus* Lw.—Pharyngeal sack.

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ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XVIII   No. 2

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STUDIES ON GREGARINA BLATTARUM WITH PARTICULAR REFERENCE TO THE CHROMOSOME CYCLE

WITH SIX PLATES AND
TWO TEXT-FIGURES

BY

Victor Sprague

CONTENTS

ACKNOWLEDGMENT

INTRODUCTION

THE SUBJECT of these studies, *Gregarina blattarum* von Siebold, is one of the most common and widely known of the Sporozoa and has been studied by many investigators. Many phases of its life-cycle have, nevertheless, received but scant attention and are not at all understood. One particularly neglected, but very significant, period is that which involves syngamy and the meiotic phenomena. The present investigation deals principally with that period but also includes an account of the process of encystment and the development of the cyst.

HISTORICAL REVIEW

A number of early workers probably saw *Gregarina blattarum* before it was actually described but did not recognize its true nature. Among them was von Siebold (1837), who observed ovoid bodies in the gut of *Blatta orientalis* Linnaeus, which he thought were insect eggs. At that time he noted their resemblance to *Gregarina ovata* Dufour, 1828, the first gregarine ever to be named and described. Later, after observing the ovoid bodies in locomotion, von Siebold (1839) changed his earlier view and concluded that they were peculiar helminths. He then gave the original description, including observations on morphology, locomotion, and syzygy, and proposed the name of *Gregarina blattarum*.

The next contribution was made by Stein (1848), who collected feces from *Blatta orientalis*, recovered mature cysts from them, and described the spores of *Gregarina blattarum*. He wrote that the spores were "tonnenförmig, 1/200''' lang und 1/570''' breit, sehr blass, aber von starken Conturlinien begrenzt . . . . Schale und Inhalt liessen sich nur bei sehr starken Vergrösserungen von einander unterscheiden." In the gut of one roach two mature cysts were found which Stein thought had been ingested with the food. One of them was ruptured and spores were seen to emerge from it. Among spores Stein observed some very young gregarines which, because of their very small size, he believed to have escaped from the spores.

Leidy (1853) characterized the genus and, not having access to the writings of von Siebold and Stein, described in detail what he believed to be a new species of gregarine from *Blatta orientalis*, calling it *Gregarina blattae orientalis*. The description included the first observation on longitudinal myonemes in gregarines. This observation was confirmed by Lankester (1863).

Schneider (1875), who gave an excellent summary of the literature on gregarines, made extensive observations on the minute structure of a

number of species and introduced a very large portion of our modern terminology. He also described and figured, for the first time, a cyst of *Gregarina blattarum* in the process of discharging its spores.

Bütschli (1881) observed the process of encystment by placing two individuals in egg albumen which, according to Watson (1916), is "a process never before seen and very rarely described since." Bütschli further studied the spores and the trophozoites of this organism and recognized, for the first time, the epimerite. It appears probable that Bütschli, as he himself wrote, was first to perform infection experiments with gregarines.

While Bütschli studied cysts in the fresh condition, Wolters (1891) used sections in his observations on the development of the cyst. He also studied the nucleus and the ectoplasmic layers of the sporodin in considerable detail.

Marshall (1893) repeated the observations of Bütschli and, in addition, made a study of the nuclear changes, including those in the developing spore. This author discovered the cross-striations in the ectoplasm of *Gregarina blattarum*.

In 1903 Crawley reported the occurrence of *Gregarina blattarum* in *Periplaneta americana* (Linnaeus) and *Blattella germanica* (Linnaeus) as well as in the original host.

Another study of the nuclear changes was made by Schiffmann (1919), who wrote, "*Gregarina blattarum* ist seit der Erkenntnis der geschlechtlichen Vorgänge noch nicht bearbeitet worden." Schiffmann outlined the general course of development but was unable to demonstrate much detail, since the section method alone, which was used in that study, probably is inadequate for revealing the more minute details of nuclear phenomena.

A short time later Jameson (1920) published a paper on *Diplocystis schneideri* Kunstler of far-reaching importance with regard to the chromosome cycle of gregarines. He found, to use his own words: "The sporoblast is a zygote. Its nucleus is formed by the fusion of the two gamete nuclei, each containing a similar set of three chromosomes. The first nuclear division of the sporoblast is a reduction division. From the spireme, which is formed during the early prophases, six chromosomes arise. These lie on an indistinct achromatic spindle and separate into two homologous groups of three, one set of three passing to each pole. A second and a third mitotic division then take place—each presenting the same number (three) of chromosomes—giving rise, finally, to the eight sporozoite nuclei. The sporozoites thus each contain three chromosomes— a single or haploid group. This is the number present again in all the nuclear divisions—including all the divisions associated with gametogenesis—of the gamont, which is the adult organism into which the sporozoite grows.

"This type of reduction division is new, and it explains in a simple fashion the odd chromosome number so common among gregarines. The number found in every division excepting the first sporoblast division is the haploid number. Only once in the whole life-cycle is the diploid number found, namely, in the first division of the sporoblast. It seems probable that a careful re-examination of gregarine life-histories, paying special attention to the sporal divisions, will reveal this to be the real method of reduction in all."

Noble (1938) has recently studied the chromosome cycle in another acephaline form in which, he believes, reduction occurs in the zygote.

Contrary to the generalization of Jameson, gametic meiosis has been observed in some genera of the Acephalina, such as Monocystis (Mulsow, 1911; Calkins and Bowling, 1926; Naville, 1927a) and Urospora (Naville, 1927).

Jameson included in his paper a list of all gregarines whose chromosome numbers were known and gave the number for each species. The monumental works of Bélař (1926) and Naville (1931) include a few additional species whose chromosome numbers have been more recently determined.

A small number of studies on the nuclei of gregarines have appeared in recent years, although much attention seems to have been given to the cytoplasm, particularly since 1926 when the admirable researches of Joyet-Lavergne gave impetus to this type of investigation. No noteworthy contribution, so far as the writer is aware, has been made for *Gregarina blattarum* since the work of Schiffmann.

MATERIAL AND METHODS

Cockroaches, *Blatta orientalis,* were collected in the fall of 1939 (September to late November) on the campus of the University of Illinois at Urbana and were kept in the laboratory in battery jars. At first, they were fed a diet of yeast, but later (in December) they were given apples instead. The latter diet has an advantage over the former in that it does not render the detection of the parasites difficult when one examines the gut contents and the feces. Furthermore, after the first part of January, 1940, there was a tremendous increase in the incidence and amount of infection, which may have had some relationship to the diet. The true cause of this increase is at present unknown, but it appears probable that the infection was built up over a period of time due to the close confinement of the hosts in the containers. From time to time cysts were placed in the food, and this was probably also a factor in the increased incidence of infection.

The host insects were examined by extracting the gut in 0.75 per cent

NaCl solution and placing it under a binocular dissecting microscope. Cysts were recovered from feces by immersing in water for a few minutes, crushing gently to avoid damaging the cysts, and picking out the latter with a pipette.

Of 810 roaches, which were examined soon after collection between late September and the middle of December, forty-five individuals or 5.3 per cent were infected. Each of the infected individuals contained from one to twelve sporadins, and a total of two cysts was found. In late November and December a few cysts were found also in the feces.

During January and February about fifty hosts were examined, and 30 per cent were found to be infected. In almost every instance of infection at this time, the mid-gut was literally packed full of parasites in all stages of development from young trophozoites to completely formed cysts. Very frequently the hind-gut also contained cysts; in one instance thirty-one cysts were obtained from this region.

Most of the cysts used in this study were collected from feces (during January and February), since all but the earliest stages are easily obtainable from this source. The feces of about one hundred roaches yielded from two hundred to four hundred cysts daily, until most of the roaches suddenly died from some unknown cause. In some instances the pellets consisted almost entirely of cysts, one such pellet containing fifty-eight normal cysts and about a dozen abnormal ones. Frequently large masses of gregarines in the vegetative stages were also noticed in the feces.

After the cysts were collected, it was necessary to keep them under conditions suitable for their normal development in order that desired stages might be obtained. In attempting to do this, several methods were tried and only one was successful. Although cysts air-dried or kept in 0.75 per cent NaCl or distilled water failed to develop, highly successful results were obtained by incubating them, at room temperature, in moist chambers constructed in the following manner: Several layers of circular pieces of towel paper were placed in the bottom of a finger bowl and moistened with water. On top of the towel paper was placed a small piece of black drawing paper. A watch glass containing cysts, without any water, was placed on top of the black paper; and the finger bowl was covered with a glass plate and sealed with vaseline. The cysts were examined from time to time with a binocular dissecting microscope and reflected light, the white cysts appearing in sharp contrast on the black paper in the background.

Cysts were removed from the moist chamber after various intervals of time, depending on the stages desired, and smear preparations and sections were made. The sectioning was done individually or in mass after fixation in the solution of Carnoy, Schaudinn, Bouin, Flemming (strong),

Zenker, Feulgen (sublimate-acetic), or Perenyi. None of these fixatives proved quite satisfactory. All of them penetrated the cyst membranes very slowly, and all except Flemming caused the majority of the cysts to explode. Flemming seemed to penetrate fairly well, but subsequent staining was unsatisfactory. Some fair preparations were obtained after Perenyi, and in instances of good fixation with Carnoy the staining was usually excellent. Sections were stained with Heidenhain's haematoxylin or subjected to the Feulgen nucleal reaction. The best section preparations were obtained by the Carnoy-Heidenhain, Carnoy-Feulgen, and Perenyi-Heidenhain combinations. Sections were found useful for determining the general course of development within the cyst but not good for nuclear detail.

For observations on the nuclear changes the smear method was used almost entirely. Smears were prepared by crushing the cysts on cover glasses, fixing in Schaudinn, Flemming, or Zenker, and either staining with Heidenhain, Giemsa, or Flemming's triple, or subjecting to Feulgen's nucleal reaction. Lang's (1936) formula was used exclusively for the mordant before haematoxylin. The best results were obtained with the Zenker-Heidenhain combination and Schaudinn followed by Heidenhain, Feulgen, or Giemsa.

For studying the process of encystment, associated pairs of gamonts, which showed by their rotating movements that they were ready to encyst, were placed in fresh egg albumen on a depression slide and covered with a cover-glass. ·Thus, the experiment of Bütschli, who also used egg albumen, was easily repeated a number of times. Attempts to obtain encystment in 0.75 per cent NaCl were unsuccessful, although the gregarines appeared to make strenuous attempts to encyst for an hour or more. Possibly a quite viscous medium is essential for the successful completion of this process, although various unknown factors may be involved.

Glossary

To avoid confusion in terminology, the following glossary is given. Some of the terms are probably new. Others have been more frequently used with regard to the metazoa, and most of them have been applied with various meanings to the gregarines and other protozoa.

Acephaline gregarine: A non-septate form; the body is not divided into protomerite and deutomerite.

Association: Two or more individuals in syzygy.

Basal disc: A hyaline, circular area in the sporoduct membrane surrounding the proximal end of the sporoduct.

Cephaline gregarine: A septate form; the body is divided into protomerite and deutomerite.

Cyst: A spheroidal body, surrounded by a resistant membrane, into which the associated gamonts develop at the beginning of the reproductive process.

Cyst membrane: The elastic, hyaline, laminated covering of the cyst.

Deutomerite: That portion of the sporadin posterior to the septum in cephaline gregarines.

Epimerite: A process at the anterior end of the protomerite by which the young trophozoite is attached to the host cell.

Gamont: The initial stage in gamete-formation; one of the individuals in an association, or in a young cyst, destined to form gametes.

Gelatinous layer: A thick, amorphous, hyaline layer of gelatinous consistency surrounding the cyst membrane.

Meiocyte: Any protoplast in which meiosis is initiated; the zygote or sporoblast in haploid gregarines.

Meiotic division: Any nuclear division involving the segregation of maternal and paternal chromosomes.

Metagamic divisions: Nuclear divisions following syngamy.

Mucoid sheath: A layer of adhesive substance covering the spore.

Myonemes: Contractile fibrils in the ectoplasm of the sporadin.

Perinuclear vesicle: A chromophobic area surrounding the nucleus of the gamete and apparently bounded by a delicate membrane.

Pregametic divisions: The series of nuclear divisions producing the nuclei of the gametes.

Primite: The anterior individual in an association of gamonts.

Protomerite: The anterior compartment of a septate gregarine.

Protoplast: A cell or any morphologically comparable unit.

Residual mass: Used here with particular reference to that viscous part of the former gamont which remains after the gametes have budded off the periphery.

Satellite: The posterior individual in an association of gamonts. There is usually only one, but more may be present.

Septum: A transverse partition dividing the sporadin into anterior and posterior compartments, the protomerite and deutomerite respectively.

Sporadin: A trophic individual after detachment from the host cell.

Spore: The body into which the sporoblast (zygote) develops.

Spore membrane: The resistant covering of the spore; sometimes called the "sporocyst."

Sporoblast: The initial stage in spore formation. In gregarines it is synonymous with zygote.

Sporoduct: A tubular structure continuous with the sporoduct membrane and serving to conduct the spores out of the cyst.

Sporoduct membrane: A membrane lying just beneath the laminated cyst membrane and containing the sporoducts.

Sporozoite: One of the eight falciform bodies developed within the spore.

Syngamy: Fusion or copulation of isogamous or anisogamous gametes; fertilization.

Synkaryon: Zygote nucleus.

Syzygy: An end-wise association of two or more sporadins.

Trailing chromosome: That chromosome which characteristically follows behind the other members of the chromosome complex in the anaphase. This has sometimes been inappropriately called the "odd chromosome."

Trophozoite: An individual in the feeding stage, either before or after the loss of the epimerite.

Zygote: The body resulting from syngamy; the sporoblast in gregarines.

Zygomeiosis: Chromosome reduction taking place immediately after syngamy in contrast to the usual meiosis which is delayed until gamete-formation.

OBSERVATIONS

VEGETATIVE PHASES

MUCH has been written on the trophic stages of *Gregarina blattarum* by von Siebold, Leidy, Schneider, Bütschli, Wolters, and Marshall. Little can be added to that subject now without undertaking intensive studies of such aspects of the problem as cytology, physiology, and statistical analysis. Any observations made on the vegetative stages in this study are only incidental, but a few of them seem worth noting.

It was observed in a number of hosts having light infections that the sporadins were unusually large. One such individual, found alone in the host, measured about 950 μ long and 550 μ wide (Fig. 1). There may be a relationship between the number of parasites and their size, although conclusive evidence on this question is lacking.

Also of interest is the fact, previously noticed by many workers, that the gregarines often become associated in pairs very soon after the loss of the epimerite. Thus individuals of all sizes, from very small (Fig. 2) to very large, are seen in association. The two members of the association are usually very similar in size, but frequently the satellite is much smaller than the primite. The reverse size relationship, as von Siebold observed, appears never to occur. These associations with unequal individuals form young cysts containing two unequal gamonts (Fig. 15). Cysts of this type provide a method of identifying primite and satellite after encystment and suggest a method whereby the resulting gametes may be studied for possible differences in structure and behavior. Sometimes two small satellites are seen on one large primite, as both von Siebold and Marshall observed (Fig. 3). The two satellites may be approximately the same size, in which case the resulting cyst contains one large and two equally small gamonts, or the two satellites may differ in size. In the latter case, the resulting cyst contains three gamonts of different size (Fig. 12). These unusual types of cysts seem to develop normally and produce typical spores.

REPRODUCTIVE PHASES

Encystment

The process of encystment and subsequent development of the cyst were so well described and illustrated by Bütschli that it is necessary here only to outline that process and mention certain new observations.

In January and February, when abundant material was on hand, hundreds of individuals, in all stages of development, were often found in the mid-gut of a single host. Many of the larger pairs were undergoing characteristic rotating movement indicating imminent encystment.

Pairs of this type, when placed in fresh, undiluted egg albumen, as described above, are easily observed while they continue the process of encystment. The two individuals glide slowly forward, both bending in the same direction, with much folding of the body wall, so that there is a tendency to move in a circle (Fig. 4). The satellite seems to be the more active of the two. While the anterior end of the primite bends to one side, the satellite pushes forward and, at the same time, brings its posterior end up toward the anterior end of the primite (Figs. 5 and 6). When these two ends are brought together, often after many unsuccessful attempts, they adhere and the pair continues to rotate (Fig. 7).

The coming together of the opposite ends of the pair apparently is not accomplished solely by active bending of the bodies. The force of the forward movement seems also to be a factor, since it tends to bend the bodies passively when the anterior end meets resistance in the medium. The bending process seems to be greatly facilitated when the protomerite of the primite collides with bits of debris in the medium, which retard the forward movement. It appears probable also that the viscosity of the medium is a factor in the passive bending. The gamonts, as stated previously, never seemed quite able to make the two ends meet when they were placed in 0.75 per cent NaCl solution, although they frequently underwent active bending and forward movement for more than an hour. If the pair, however, was placed in this solution after adhesion of the opposite ends was completed, encystment proceeded in the normal manner. In the egg albumen, on the other hand, the gamonts were able to accomplish the process from the very beginning. This may be due, at least in part, to the fact that this medium is viscous and resists the forward movement, thus supplementing the active bending of the bodies. It should be noted also that the normal habitat of this parasite is a viscous medium, the gut contents, containing much debris. It seems probable, therefore, that a viscous medium is a mechanical factor necessary for encystment, although other factors are undoubtedly involved.

When encystment occurred in egg albumen *in vitro*, it was observed that frequently no gelatinous layer could be detected outside the true cyst membrane. This layer may actually have been absent, or it may have been indistinguishable from the egg albumen.

About forty-five minutes after the beginning of encystment the true cyst membrane is being secreted, and at this time the young cyst is almost perfectly spherical in shape (Fig. 8). Then the myonemes, which are seemingly in a state of contraction during the early stages of encystment, probably relax, for the young cyst rather suddenly begins to elongate in a direction perpendicular to the plane separating the two gamonts (Fig. 9). The spherical shape of the cyst thus changes into that of a prolate spheroid. While elongation slowly continues for about thirty

to forty-five minutes, the plane between the two individuals becomes somewhat oblique to the long axis.

Shape and Size Variation of the Cysts

Bütschli called attention to the change in shape of the young cyst, remarking that it gradually assumes an ovoid form "welche die ausgebildeten Cysten stets zeigen." This author apparently did not observe a sufficient number of cysts formed under normal conditions to notice that they are, on the average, much less elongated than those formed under experimental conditions. If one observes a great number of the former, some are seen to be very long, others almost perfect spheres, and the majority are between these two extremes.

In order to determine mathematically whether there is a relationship between the shape of the cyst and the conditions under which encystment occurs, the following procedure was followed: twenty-five cysts formed within a single host gut in the normal manner were obtained, and fourteen pairs of mature gamonts from the same host were allowed to encyst in egg albumen. The cysts of the two groups were measured, and the ratios of the long and short axes were determined and averaged for each group. The average ratio for the former group was found to be 1.22, the range being from 1.1 to 1.4. The ratio for the latter group averaged 1.76 and ranged from 1.3 to 2.0. These figures seem to be significant. They apparently indicate that an important factor in causing the extreme variation in shape is the immediate surroundings at the time of encystment. Cysts of the spherical type are probably formed in such close confinement that elongation at a certain critical time is mechanically impossible. Longer ones probably are not so closely confined during formation, and thus are able to expand upon the relaxation of the myonemes of the gamonts while the cyst membrane is still in a plastic condition.

Marshall observed some pairs in syzygy which were long and thin and others which were short and compressed. He thought that this fact explains the difference in shape of the cysts, elongated ones developing from the former and spherical ones from the latter.

The membrane of an extremely long cyst has a noticeable lack of uniformity in thickness, being much thicker at the ends than in the middle region (Fig. 11). This can probably be attributed to the fact that the extreme elongation inhibits the normal rotating movements of the individuals within the cyst, thus preventing an even distribution of the substance secreted to form the membrane. Such cysts do not often develop to maturity, for the membrane usually ruptures at the thin places. Cysts with ruptured membranes seem never to continue their development.
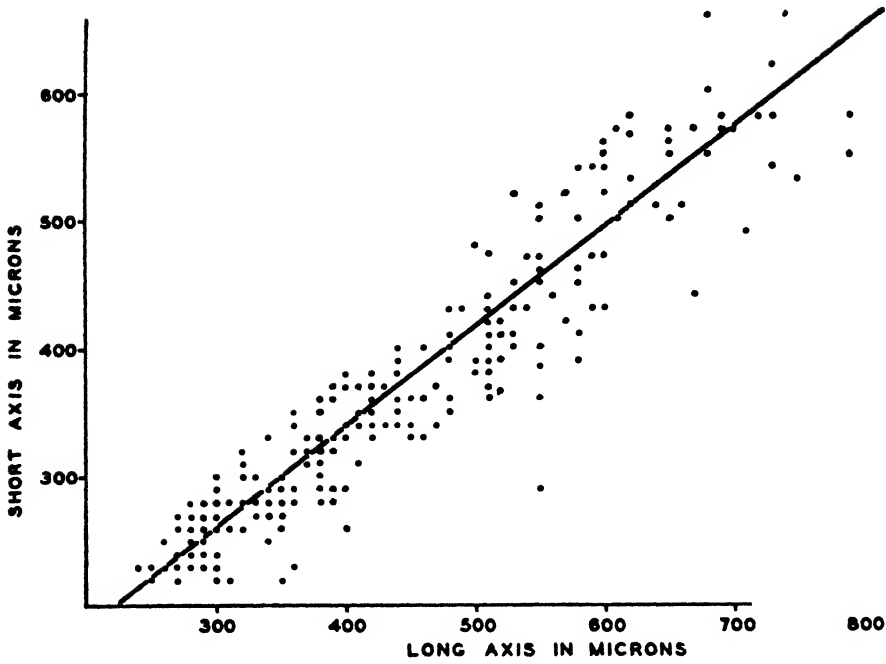
TEXT-FIG. I.—Scatter diagram showing a positive correlation between the long and short axes of a random sample of 259 cysts.
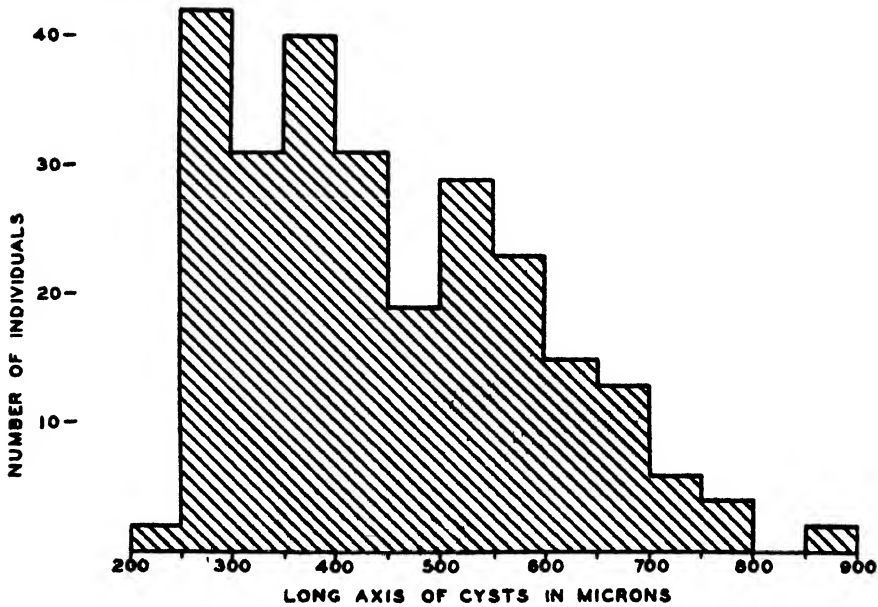
TEXT-FIG. II.—Histogram showing size distribution, based on the long axis, of a sample of cysts.

To obtain further information on the variation in shape, 259 cysts in a random sample were measured in microns; and the long axes were plotted against the short axes (Text-fig. I). The points on the resulting figure are seen to fall about evenly on the two sides of a straight line running through them. (A number of the points represent two or more individuals.) This distribution indicates that there is a definite relationship between the long and short axes regardless of the size, all ranges of variation in shape being found in each size group. In other words, there is a positive correlation between the long and short axes, the one tending to vary in direct proportion to the other.

Having demonstrated a straight line relationship between the two axes of the cysts, it is now possible to compare accurately the sizes on the basis of either of the two dimensions. Accordingly, the size groups (based on the long axes) were plotted along the abscissa, the frequencies were plotted along the ordinate, and a histogram was constructed showing the size distribution (Text-fig. II). An extremely rapid rise in frequency is shown, plainly indicating that encystment seldom occurs until the gamonts have attained a rather definite minimum size. This confirms the opinion of Watson (1916) who stated that "only the large individuals in any case may be expected soon to form cysts." Size is thus correlated with gamont maturity, although suitable physiological conditions must undoubtedly exist before encystment can take place. The histogram further shows, as one would expect, a tendency toward a gradual decrease in frequency, while size further increases, suggesting that encystment may be delayed by various physiological factors after mature size has been attained. At two points there are sudden drops in frequency which are difficult to interpret. There are a number of possible explanations, although it must be admitted that none of them is demonstrated. It is altogether possible that, in view of certain nuclear phenomena described later, two or more varieties of the organism are represented. Furthermore, the sample may not be representative or sufficiently large. Again, some of the irregularities may be due to large cysts formed by three or more individuals. And, finally, there are many unknown physiological and environmental factors involved.

The results of the present incomplete investigation suggest the desirability of a thorough-going statistical study in an attempt to discover some of the factors contributing to the size variation of the cysts of *Gregarina blattarum*.

Gross Features of Cyst Development

Changes occurring in the cyst from the time of its formation to the appearance of gametes on the periphery were not observed. Bütschli found that the boundary between protomerite and deutomerite disap-

peared within three hours. The next change he noticed was the appearance of gametes (which were considered by Bütschli and other workers to be young spores) on the periphery about sixteen to twenty-four hours later. In the meantime profound changes in the ectoplasm layers of the gamonts have taken place. These layers have disappeared, in a manner which is not clear, and in their place a layer of gametes has appeared. The observations of the present author on the course of further development will now be described.

The peripheral layer of gametes has been aptly described as resembling a layer of columnar epithelial cells, for they are so crowded together that they have a columnar appearance (Figs. 12 and 16). This gamete layer is very translucent and contrasts sharply with the opaque granular mass which it encloses. Each residual mass is completely covered by the gamete layer, although Bütschli stated: "Auf der Vereinigungsfläche der beiden encystirten Individuen scheint es wohl sicher nicht zur Bildung von Sporen zu kommen." It is difficult to understand why Bütschli failed to see the gametes, which he mistook for spores, on the contiguous sides of the two individuals, for they are as conspicuous there as elsewhere and are seen not only in living material but also in sections. Illustrations of Marshall also seem to show this condition. It is, in fact, these gamete layers, and nothing else, which separate the two individuals at this time and prevent their fusion. As was stated above, the fate of the original ectoplasmic boundaries seems to be, for this species at least, unknown.

Before the gametes begin to separate from the residual mass, the two halves of the cyst contents fill the cyst entirely and are so pressed together that their contiguous sides are flat surfaces (Fig. 16). The next change is a slight rounding up of the two masses so that a space filled with aqueous fluid appears between them. At the same time, gametes begin to separate from the periphery, round up, and pass out into the aqueous fluid (Fig. 17). The first gametes to separate are those at the edge of the flat surface because, perhaps, they are under a smaller amount of pressure than the others which are closely pressed against the cyst membrane. In the cases observed it was often evident that activity appeared in one end slightly sooner than in the other. This may or may not indicate a sexual difference. As was suggested above, it may be possible to answer this question by observing a cyst formed from a large primite and a small satellite, in which case either of the encysted gamonts can be identified.

As the gametes begin to separate from the edge of the flat surface, each central mass becomes slightly more rounded, thus releasing pressure between the two masses. Consequently, more and more of the gametes in

that region break off. These gametes seem always to move outward toward the cyst membrane and then toward the end of the cyst.

As indicated above, the peripheral layer of gametes around each residual mass seems to act as a cellular membrane which, while intact, encloses that mass and prevents its fusion with the other. When this membrane breaks down, however, the residual masses are no longer confined and they begin to flow into one another with long, irregular extension of their substance (Fig. 18). The flowing together of this substance in the middle region releases pressure on the ends and the gametes in those regions immediately pinch off and pass out into the clear liquid. Whereas the movement of gametes was previously from the middle region toward the ends, there is now a reversal of direction for a short time; but soon no constancy of direction is seen. About ten minutes later the two residual masses have fused into a single viscous mass surrounded by a watery liquid containing gametes (Fig. 19).

The cause of these activities is quite unknown but it may be permissible to suggest an hypothesis. The layer of gametes surrounding the viscous inner mass, which is a colloidal suspension, may permit, or actively cause, the passing through of water while retaining the suspended materials. This loss of water from the inner mass results in a decrease of size and a consequent tendency of the mass to round up. The gametes then pinch off and float out into the watery liquid. The two residual masses, now being in close contact, fuse into one.

After a time, not accurately determined but certainly nearly an hour, the aqueous fluid containing gametes and the residual mass, being no longer separated by any sort of boundary, merge into a single mass which is uniformly granular and fills the entire cyst (Fig. 20). Possibly the pairing of gametes occurs while they are free in the aqueous medium, but this point was not determined.

No conspicuous changes are noticed until the next day when the basal discs of the sporoducts are plainly seen (Fig. 21). These structures are just as Bütschli described them, consisting of circular areas free from large granules like those all around, but containing very small granules which radiate out from the center. In the center is the lumen of the sporoduct. It is at this time that the sporoducts are most easily counted. If the cysts are placed on a slide and rolled with a sidewise pressure on the cover glass, the sporoducts can be counted with a fair degree of accuracy. By this method the sporoducts of a random sample of twenty-four cysts of all sizes were counted. The number was found, as Bütschli observed, to be roughly in proportion to the size of the cyst, varying from five to thirty. The average was thirteen. Bütschli gave the number as three to about a dozen, and Watson gave eight to ten.

During the next two days the only noticeable change is a decrease in the opacity of the cyst, as observed by Bütschli, which seems to be due to a decrease in the paraglycogen content and also to the translucency of the spores in the center. Sometimes the cyst becomes so translucent that the individual spores can be plainly seen within. Then, about forty-eight hours after the sporoducts are first seen, the latter break through the cyst membrane (Fig. 22), and the spores are discharged in long chains. The time given here agrees with the observation of Bütschli, but Schiffmann found that the sporoducts are everted in seven days. It is doubtful whether the moist chamber used by the latter author was of a type to provide the best conditions for development, for the surface of the cysts in that chamber became irregular by the time the sporoducts were first seen. In the present study the external appearance of the cysts seemed to remain absolutely unaltered up to the time of maturity.

Sporoducts were studied by Stein, Schneider, Bütschli, Schiffmann, and others. The observations of Bütschli were particularly thorough, and nothing can be added to his description at this time. The sporoduct is a tapering tube about 200 μ long and with a bulbous enlargement near its base (Figs. 22 and 25). This tube is continuous with a thin membrane, which Bütschli has called the sporoduct membrane, just inside the cyst membrane proper. The time and manner of formation of the sporoduct membrane seems to be completely unknown.

Mechanism of Sporoduct Evertion

The writer is not aware that anyone has yet explained how it is possible for the delicate sporoduct to make its way through the thick, resistant cyst membrane. In the present study certain observations were made which seem to provide an explanation of that phenomenon. When a cyst approaches maturity the basal disc of the sporoduct seems to become slightly raised above the surrounding surface of the sporoduct membrane, forming a small convex protuberance (Fig. 23). The cyst membrane at this point is slightly thinner than elsewhere and may also be raised above the adjacent surface. The thin area in the membrane is very conspicuous when a sporoduct fails to break through due to the release of the internal pressure when other sporoducts are everted (Fig. 24). If one is so fortunate as to be observing the cyst at exactly the right moment the basal region of the sporoduct is seen to burst suddenly through the weakened area in the cyst membrane; and, by rapidly turn ing inside out, the sporoduct becomes completely extended to the outside. A few droplets resembling oil globules then pass out of the sporoduct and are immediately followed by the spores, which are rapidly discharged

in long chains. The oil droplets possibly serve as a lubricant to minimize friction between the sporoduct and the spores; for the latter, after their discharge, are actually covered by an oily film.

When the thin areas in the cyst membrane were first observed, it was suspected that a lytic action occurs in the region of the basal disc. To obtain information on this question various pH indicators were added to water containing cysts which were ready to discharge their spores. These indicators were unable to penetrate the intact cyst membrane, but they did reach the inside of the cyst when some of the sporoducts were everted. Upon the addition of neutral red the basal disc and the proximal portion of the sporoduct became very dark red, the color being much less intense in the distal region (Fig. 25). A number of dark red granules were also seen in the sporoduct membrane, and others were scattered throughout the interior of the cyst (Figs. 24 and 25). Bromthymol blue gave comparable results, the color obtained being yellow instead of red. No color changes were noticed with methyl red, phenol red, or brom-cresol purple. On the basis of the color changes with the indicators, it is concluded that the reaction in the basal region of the sporoduct is decidedly acid.

These observations lead to the following hypothesis, which is offered to explain the mechanism of sporoduct evertion: Since acid is present in the basal portion of the sporoduct, there may also be an enzyme in that region acting in the presence of the acid to dissolve, and therefore weaken, the adjacent area of the membrane. The latter, being very elastic, constantly exerts a relatively enormous pressure on the contents within, and, after the enzymes have acted sufficiently, the pressure on the contents forces the sporoduct out through the weakened area. The great pressure exerted by the elastic membrane also adequately accounts for the force which expels the spores.

The elasticity of the cyst membrane is easily demonstrated in a number of ways. If a normal cyst is ruptured, the contents are expelled; and the cyst immediately decreases in size. At the same time, the membrane, which was formerly thin and homogeneous in appearance (Fig. 26), becomes very thick and is conspicuously stratified (Fig. 27). Furthermore, if the membrane is stretched with needles and then released, it snaps back to its former condition in a manner which reminds one of a rubber band. Finally, when the spores are released from the mature cyst, the latter decreases greatly in size (Figs. 32 and 33), and the membrane becomes very thick. Both Bütschli (1881) and Schellack (1912) noticed the elasticity of the membrane and emphasized its role in discharging the spores, but neither attempted to explain how the sporoducts make their way through the membrane.

The Mature Spore

Shape.—The spores of *Gregarina blattarum* have been described as being barrel-shaped and with truncate ends. Stein (who was the first to describe the spores), Schneider, Bütschli, Marshall, Ellis, Watson, and Schiffmann have given essentially the same description as to the shape. The fact is that, although the spores appear truncate (Fig. 28), they are, in reality, broadly rounded at the ends. The truncate appearance is due to the presence of an external layer of mucoid substance which forms a sheath over the true spore membrane and fills up the space between the rounded ends of the contiguous spores in the chain.

The presence of this sheath is demonstrable in a number of ways. It can be directly observed in optical section (Fig. 29), for the sheath, being less hyaline, appears slightly darker than the true spore membrane. This is particularly evident at the ends of the spore where the sheath is thicker; here it often forms a ring-shaped elevation around the end of the spore. Bütschli called attention to the fact that the terminal portion of the spore covering is darker than the rest, but he did not recognize the significance of this difference. The substance covering the spore dissolves in either dilute or glacial acetic acid. Spores thus treated show well rounded ends (Fig. 30). Finally, when fresh spores are placed under a cover-glass and a slight pressure is exerted on them, the sheath is often removed and is seen as a delicate membrane lying beside the spore, the latter having broadly rounded extremities. The source of the mucoid sheath is probably the viscous mass of mucous substance in which the spores are imbedded during their development.

In cross section the spores appear to be perfectly round, as seen in both fresh and stained preparations. The sides of the mature spore are usually somewhat convex, but not infrequently they appear perfectly parallel to each other. The spore thus varies in shape from an ellipsoid to a cylinder with rounded ends.

Size.—Stein gave the size of the spore as "1/200''' lang und 1/570''' breit" (which is about 10.8 μ by 3.8 μ) ; Ellis gave 4 μ by 8 μ; Watson "8.3 by 3.7 and 4 by 8 μ." In the present study fifty fresh, mature spores from a single cyst were measured in 0.75 per cent NaCl; and the averages of the long and short axes were found to be 8.77 μ and 4.30 μ respectively. These figures are in good agreement with those given by all other workers except Stein, and no explanation of this difference can be offered. It is possible that spores in different cysts differ in size, but this question remains to be investigated.

Structure.—The mature spore consists of the mucoid sheath described above, the true spore membrane, and the contents within. The membrane itself is very hyaline, uniformly rather thick, plainly double contoured,

and with no trace of any surface markings (Fig. 30). Internally, the developing spore appears uniformly structureless except for a large fat droplet which stains dark red with Sudan III. Later, this large droplet breaks up into a variable number of smaller droplets (Fig. 30). At maturity two small refractile spherules, of undetermined nature, are usually seen within the spore, one lying near each end. Frequently faint spiral striations are also seen within the mature spores. The striations at a higher optical level form crosses with those at a lower level. These striations probably represent either the eight sporozoites within or the eight long nuclei of the sporozoites. Attempts to determine their true nature with acidified methyl green and various vital stains were unsuccessful, since the membrane of the spore is very resistant to the penetration of stains.

Spore Chains.—A number of workers have noticed that the spores, as they emerge from the cyst, are associated in long chains; but no one seems to have noted the extremely great length which a single spore chain may attain. The lengths of the chains depend somewhat on the medium in which the expulsion of the spores occurs. In water, relatively short chains are formed; but in air, with the humidity at the saturation point, the chains formed are remarkably long (Fig. 31) and contain many thousands of spores. The idea was conceived that if the chains were straight, it would be easy to measure their lengths. Some cysts were then placed on a glass plate, to which they readily adhered; the excess of water was removed with filter paper; and the plate was inverted over the mouth of a large glass vial containing a small amount of water to maintain a high humidity. When the spores were discharged, they extended directly downward as long straight threads resembling cobweb. Threads as long as 87 mm. and containing approximately ten thousand spores were obtained.

When a large number of cysts from feces are placed in the moist chamber and left to mature, they appear to the unaided eye, on the third day, as if entirely overgrown with fine white threads of mold. These white threads, when highly magnified (Fig. 34), are seen to be chains of the spores. As they pass out of the cyst and come in contact with objects in the vicinity, they often become arranged in large coils, the coils having many turns and thus containing many thousands of individual spores (Fig. 35).

One at once wonders how it is possible for the spores to become associated in such extremely long chains. It is inconceivable that chains of such length are pre-formed within the cyst, although sections of mature cysts show that many of the spores do lie end to end. The probable explanation is that the shorter chains become united as they pass out through the sporoduct. The force exerted by the contracting cyst mem-

brane upon the spores as they pass out presses them together, and the mucous substance covering the spores is sufficiently adhesive to cement them to one another.

When spores discharged into the air are placed in water, they strongly resist wetting and tend to collect on the surface films of air bubbles under the cover glass (Fig. 36). This phenomenon indicates that the spore has a film of oil on the surface. This oil, as was already mentioned, probably serves as a lubricant to aid the spore in passing through the narrow lumen of the sporoduct (Fig. 22).

Nuclear Phenomena

An investigation of the entire nuclear cycle of a gregarine is an enormous task and has been undertaken in only a few instances. In the case of *Gregarina blattarum,* by far the greater part of the previously published observations have concerned the earlier stages. Von Seibold and Leidy made observations on the nucleus of the living sporadin. Bütschli studied the nucleus in the trophic stages and the young cyst, using living material. Wolters studied some of the stages within the young cyst, using sectioned and stained material. Both Marshall and Schiffmann made a number of observations on the nuclear changes throughout the life cycle of this sporozoan. Our knowledge of most of the stages is still quite fragmentary, however, and we have by no means a connected account of the nuclear cycle.

Although it is highly desirable at this time to investigate the entire cycle, technical difficulties involved in preparing good sections of the cysts and a limited amount of time prevent such a study. The present investigation, therefore, is largely confined to those extremely interesting and critical stages which occur in the developing sporoblast and which involve syngamy and the meiotic phenomena. These stages have not yet been worked out in detail for any cephaline gregarine, and conclusions with regard to the time and manner of chromosome reduction in this group have previously been based largely on a priori evidence and analogy. An accurate knowledge of the chromosome cycle requires an understanding of the meiotic division and the stages immediately preceding and following them. Furthermore, a knowledge of these stages probably includes the essential features of a chromosome cycle. It seemed, therefore, most desirable, in view of the fact that meiosis in some of the Acephalina is known to be zygotic, to give particular attention to the chromosome behavior in the developing sporoblast.

Pregametic Divisions and the Gametes.—The pregametic nuclear changes were studied only sufficiently to determine with relative certainty the number of chromosomes involved and the nature of the nuclear divi-

sions. No attempt to give a complete account of the nuclear changes previous to gamete formation is made.

The chromosomes are most easily distinguished in the anaphase. At this time three chromosomes are seen going into either daughter nucleus (Fig. 37). Two are identical in appearance, being very small and almost spherical. The third is considerably elongated. These three chromosomes have a very characteristic arrangement in the anaphase; the two small ones lie side by side and migrate in advance, while the third trails behind. The latter has frequently been called the "odd chromosome," since it differs in appearance from the other two. This designation is, however, inappropriate, as Jameson has pointed out, for it implies that the other two chromosomes constitute a pair. The fact is that if subsequent events are correctly interpreted, all three of the chromosomes are "odd" in the sense that none of them is paired. Very frequently the long chromosome appears to be more closely associated with one of the small ones than with the other, but this relationship is not always evident.

For the sake of convenience, the chromosomes may be numbered on the basis of their appearance in the anaphase. Throughout the following description the long chromosome will be designated as number 3, the short one nearest to it will be called number 2, and the other short one number 1. It is true that the basis for distinguishing 1 and 2 is very flimsy, for the spatial relationship of these two to 3 may not be constant and is certainly not always apparent. But since some method of designation is almost indispensable for purposes of description, the only one available at the present time is used.

The anaphase chromosomes move farther apart (Fig. 38) and merge into a small amorphous granule in the telophase (Fig. 39). This granule transforms itself into a vesicular nucleus (Fig. 40) from which the prophase chromosomes of another division emerge (Fig. 41). Finally, after an undetermined number of divisions, these nuclei become the nuclei of young gametes (Fig. 42) which bud off from the periphery of the former gamont.

The gamete, at the time it separates from the parent mass, is a small pyriform body, about 3 μ by 1.5 μ, with reticulated cytoplasm and a vesicular nucleus near the anterior end (Fig. 43). Very frequently the nucleus appears to be nothing but a small crescent-shaped chromatic granule lying with its convex side toward the anterior end of the gamete. On the other hand, it often appears to be a small vesicle surrounded by a delicate nuclear membrane, with most of the chromatin collected into a large mass on one side. Schiffmann thought that most of the chromatin collects on one side of the nucleus and is then thrown out, the process constituting a "primitive Reifeteilung." Nothing resembling this process

was seen during the present study. Nor was extranuclear chromatin seen in the gamete, although, according to Jameson, a number of workers have reported extrusion of a chromatin granule from the nucleus of the gamete in various species of Gregarina.

The newly formed gametes round up almost immediately, and both the nucleus and cytosome begin to increase in size. Growth continues until the original diameter of the gamete has increased by about one-half. During the increase in size, and probably correlated with it, a large vesicle appears around the nucleus (Fig. 44). This perinuclear vesicle is probably bounded by a delicate membrane. Both the nucleus and perinuclear vesicle are eccentrically located in the gamete, and the nucleus lies on the outer side of the vesicle with its chromatin granule directed anteriorly. Sometimes it seems that very faint threads can be seen radiating out from the chromatin granule into the karyolymph. These may actually represent the chromonemata of the future chromosomes. And, as later events indicate, the chromatin granule itself is probably a reservoir of nucleic acid which supplies the chromophilic component of the chromosome matrix. All the gametes appear to be morphologically alike, although a detailed cytological study might reveal differences in the nuclei or in the cytoplasmic components. Behavior during syngamy, however, suggests physiological differences in the copulating gametes.

Syngamy, Synapsis, and the First Metagamic Division.—At the beginning of syngamy two gametes come together in such a manner that a point slightly to one side of the nucleus on one individual comes in contact with another individual at an exactly opposite point on the other side. The posterior gamete, which is the more active one, may be designated, for the sake of convenience, as male and the other female. Cytoplasmic fusion of the two gametes then follows (Fig. 45). Soon the two perinuclear vesicles fuse into one, and the male pronucleus moves up toward the female one while the latter remains stationary (Fig. 46). The two pronuclei thereby come to lie in a common perniuclear vesicle, the membrane of which serves as the nuclear membrane of the future synkaryon.

During or at the end of the period of migration of the male pronucleus, its membrane breaks down and an unraveling of its three chromosomes occurs (Fig. 47). In some cysts the male pronuclei seem to behave quite differently. In such cases the individual chromosomes can rarely be distinguished (Fig. 48), but are typically associated together in the form of a more or less complete loop posterior to the female pronucleus (Fig. 49). This type of behavior could not be reconciled with that described above and may indicate that two different varieties of *Gregarina blattarum* are involved.

Immediately following or overlapping the change in the male pro-

nucleus, three short and coiled chromosomes become distinguishable in the female pronucleus; the membrane of the latter breaks down (Fig. 50); and three relatively long leptotene threads emerge (Fig. 51). It is thus evident that a complement of three chromosomes is contributed to the synkaryon (zygote or sporoblast nucleus) by each of the two copulating gametes. The haploid number is, therefore, three, and the diploid number is six.

The three chromosomes of each haploid complement are typically close together at one end (Fig. 51). Then the two complements come together in a polarized arrangement resembling that which is, according to Wilson (1925), common in the early prophase of the first meiotic division in animals (Fig. 52). The polarized chromosomes typically lie in the same position as that occupied by the female pronucleus at the beginning of syngamy, for that nucleus never changes its orientation throughout the process. In other words, the six chromosomes are so polarized that, if seen from a side view, all are directed toward such a point on the anterior end of the zygote as to form an angle of about forty-five degrees with the long axis.

At about the time the leptotene threads attain their maximum length they arrange themselves into pairs which are polarized as before (Fig. 53). This pairing probably is a true synapsis involving the association of homologous chromosomes of maternal and paternal origin. The two synaptic mates in a given pair look identical, and corresponding chromomeres can frequently be distinguished on them (Figs. 53 and 54). Further study of the chromomeres may possibly enable one to identify each of the three chromosomes at this stage.

The zygonemata enter into a typical pachytene stage by becoming shorter and thicker (Fig. 54). One pair, in the pachytene stage, is characteristically much thicker and smoother in outline than the other two and lies close to the nuclear membrane near the anterior end of the zygote. The pair which thus appears different from the other two probably represents chromosome number 3, although this point has not definitely been established.

A diplotene stage was not distinguished, although each synaptic mate has presumably become double by a longitudinal splitting by about this time.

The chromosomes continue to become shorter and thicker, and lose their polarization (Fig. 55); the definitive tetrads become arranged around the periphery of the nucleus (Fig. 56). At this stage each tetrad appears to consist of two parts, but a quadripartite composition is assumed because of the interpretation which the author places upon subsequent observation. The assumption is admittedly based, in part, on analogy with the condition known to exist in many of the metazoa. The

author can only point to the difficulties encountered in studying the relatively large chromosomes of the metazoa, and claim justification for frequently being unable to observe directly the actual conditions in structures which approach in smallness the limits of visibility.

The next change is a precocious disjunction in tetrads 1 and 2, so that four dyads and one tetrad (number 3) are seen near the periphery of the nucleus before the nuclear membrane breaks down (Figs. 57 and 58). The tetrad is not always distinguishable; but when it is properly oriented, it appears V-shaped (Fig. 58).

After the breakdown of the nuclear membrane the chromosomes usually lie in a compact clump, so that the individual chromosomes are rarely distinguishable (Fig. 59). Occasionally it can be seen that about this time the chromosome complex consists of a V-shaped tetrad (number 3) and two groups, each containing (probably) dyads 1 and 2 lying side by side (Fig. 60). A "typical" equatorial plate does not occur, because disjunction of two of the three tetrads takes place before the metaphase. No trace of an achromatic figure was seen at this or any other stage.

In the early anaphase (Fig. 61) dyads 1 and 2 of one set remain stationary, and those of the other set begin to migrate along an axis diagonal to the long axis of the sporoblast. The V-shaped tetrad (number 3) lies between the two groups of dyads. The dyads continue to migrate, and the two arms of tetrad number 3 move apart (Fig. 62).

During the anaphase a diamond-shaped clear space frequently appears in the region where dyads number 3 are still joined at one end (Fig. 63). Delayed disjunction in this region probably results in a force of repulsion along the equational plane, making all four chromatids distinguishable. At no other stage is the bivalent nature of the dyads apparent.

As the anaphase progresses, the direction of migration, which was at first diagonal, changes so that the two groups of dyads come to lie exactly opposite one another in the two ends of the sporoblast. Meanwhile, a very fine but distinct and dark-staining thread is frequently seen extending between the two number 3 dyads as they move apart (Figs. 64 and 65). In the anaphase, when the three chromosomes are most easily distinguished, they are obviously much larger in the first metagamic division than in any other division. This is due, very likely, to their bivalent composition.

In the telophase a vesicular nucleus is reconstructed with the bivalent chromosomes lying on the periphery (Figs. 66 and 67). The individual chromosomes then become indistinguishable, and the interphase condition results (Fig. 68). The nucleus in the interphase is vesicular, faintly reticulated, and has a number of small chromatin granules scattered

around the periphery. Quite a complete reorganization is thus seen to occur at the end of the first division, resulting in a relatively long interphase.

It is evident from the foregoing account that the first metagamic division is a meiotic division. The zygote (sporoblast) nucleus is diploid, each gamete having contributed a haploid set. Synapsis of homologous chromosomes occurs and is followed by tetrad formation and disjunction. Each daughter nucleus resulting from the first metagamic division contains the haploid number (three) of bivalent chromosomes.

Second Metagamic Division.—In the prophase of the second division the chromosomes emerge from the interphase as relatively long threads lying on the periphery of the nucleus (Fig. 69). The number present at this time is difficult to determine but is sufficiently large to demonstrate that the bivalents have already separated into univalents, except number 3 in which separation occurs in the anaphase. The probable condition is that four univalents and one bivalent are present. Sharp (1934) says: "In the prophase of the second meiotic division the condensing chromosomes appear characteristically in the form of threads or rods, still associated in dyads at their attachment regions but diverging widely elsewhere." Since no spindle fibers and therefore no attachment regions seem to occur here, the chromatids, as one would expect, seem to separate completely in the prophase.

A "typical" metaphase does not seem to occur. The nuclear membrane breaks down long before the chromosomes have reached their definitive form, and the chromatin threads become clumped together in a confused mass (Figs. 70 and 71). This stage resembles the metaphase of the first division but is much more confused, and the chromosomes are relatively longer and thinner. The long threads then condense and assume their final form (Fig. 72), but it is difficult to distinguish any orderly arrangement before the anaphase.

The early anaphase in the second division (Fig. 73) resembles very closely that in the first except that the chromosomes, being now univalents, are smaller. The direction of migration is diagonal as before; chromosomes 1 and 2, lying side by side, move ahead while 3 trails behind. The chromosomes do not come together in such a way that one end of each meets an end of the other two (see Fig.. 66) ; but they arrange themselves in the form of an angle, number 2 being at the corner and 1 and 3 forming the sides (Fig. 74).

In the telophase the three chromosomes fuse (Fig. 75) ; the angle becomes bent into a half circle and finally forms a complete circle (Fig. 76). Immediately upon the formation of the complete circle, the nucleus is transformed into a sphere. The resulting interphase nucleus (Fig. 77)

becomes a vesicle with chromatin granules scattered on a faint reticulum. No explanation as to the manner in which the circular nucleus becomes transformed into a vesicular one can be offered at this time.

The termination of the second metagamic division marks the end of the meiotic phenomena. The zygote is a meiocyte; and the first division involves synapsis, tetrad formation, and disjunction. In the second division the two chromatids in each dyad separate; and to each of the resulting four nuclei a haploid complement of univalent chromosomes, like that in the gamete, is restored.

Throughout the preceding description of the meiotic divisions it has been assumed, for the sake of convenience, that the first division is disjunctional and the second equational. Actually, the reverse condition may hold true; or it may be that each of the divisions is disjunctional for some elements of the complex and equational for others. Sharp states: "The four chromatids composing a tetrad are ordinarily similar to one another in appearance when fully condensed, so that it is difficult or impossible to determine by direct observation whether the separation in the first anaphase is along the synaptic or along the equational plane . . . . Furthermore, since the several tetrads in one mitotic figure may behave differently in this respect, each of the two mitoses in such cases may be disjunctional for some elements and equational for others. Taking the chromosome complement as a whole, the disjunction of its homologous elements and the equational separation of their halves are complete only at the conclusion of the second mitosis."

Third Metagamic Division and Subsequent Nuclear Changes.—The prophase chromosomes of the third metagamic division emerge from the preceding interphase as three polarized strands (Fig. 78). It is difficult to understand how this arrangement is possible, since the chromosomes went into the previous telophase in the form of a ring; but the answer probably depends on an explanation of the process involved in the transformation of the telophase ring into the interphase vesicle. No explanation of these phenomena is suggested. The nuclei are considerably smaller than in the two previous divisions and little detail can be distinguished. In the later prophase the chromosomes are usually seen as three relatively long threads all lying parallel to one another (Figs. 79 and 80).

The metaphase resembles that in previous divisions. After the breakdown of the nuclear membrane (at an undetermined time), the chromosomes lie in a confused clump (Fig. 81). They are not individually distinguishable until the anaphase begins.

In the anaphase four groups of small chromosomes (representing the four dividing nuclei) are seen, each with the characteristic arrangement seen in earlier nuclear divisions. Chromosomes 1 and 2 migrate ahead in an oblique direction while 3 trails behind (Figs. 82 to 84). The late

anaphase is like that in the second, the chromosomes being so arranged as to form an angle.

The three chromosomes in each set become fused in the early telophase to form a bent rod (Fig. 85). The rod becomes further bent to form an incomplete circle (Fig. 86), and then the two ends come together and make a complete circle (Figs. 87 and 88). The circles lie in two groups of four each near the two ends of the spore. Up to this point the third telophase resembles the second; but here the resemblance stops, for the nuclear ring does not become transformed into a vesicle.

As the telophase reorganization continues, two conspicuous granules appear on each ring (Fig. 89). The two granules are on opposite sides of the ring, and the latter is oriented in such a way that a line passing through the two granules is parallel with the long axis of the spore. Usually one granule is plainly larger than the other. This is particularly evident when the nuclear ring lies on edge (Figs. 88 and 89). The smaller of the two granules is directed toward the end of the spore in some cysts, although the reverse orientation occurs in the spores of other cysts and is described later. Judging from the appearance of the nucleus during the telophase reorganization, it seems probable that the larger granule represents the bulk of the chromatic substance of chromosomes 1 and 2 combined, while the smaller represents that of chromosome 3.

The next change is an elongation of the nuclear rings. Each transforms itself into a long oval with a chromatin granule at either end (Fig. 90). The ovals, in a manner not clear, then change into dumbbell-shaped rods which are usually plainly larger at the inner end than at the outer end (Fig. 91). Finally, the rods become further elongated and come to lie in a spiral arrangement around the peripheral region of the spore contents (Fig. 92). Since all the nuclei are spirally arranged in the same direction, those in a higher optical plane typically lie across those in a lower optical plane. Previous workers seem to have overlooked the elongated condition of the sporozoite nucleus in *Gregarina blattarum*, although Prowazek (1902) has observed a similar shape and arrangement of the nuclei in the spore of *Monocystis agilis* Stein.

No further normal nuclear changes were observed, but in mature cysts the great majority of the spores contain degenerating nuclei. The chromatin in these degenerate spores is seen in scattered masses inconstant in size, number, and arrangement. This fact may indicate that the spores remain viable for only a very short time after maturity, though experimental data on the viability of the spores is lacking. Many of the mature spores show no trace of any internal structure by any of the methods used. This may be due, at least in part, to the inability of the stains to penetrate the resistant spore membrane.

At no time were the cytoplasmic boundaries of the individual sporo-

zoites observed with certainty, although each spore is believed to contain eight sporozoites. As stated above, mature spores in the living condition frequently show faint spiral striations. Whether this appearance is due to the sporozoites or to the eight long spirally arranged nuclei is uncertain.

The nuclear phenomena in the final stage are in some instances quite different from those described above. In some cysts all the eight nuclei in every spore lie at or near the center of the spore. In such cases the larger chromatin granule is directed not toward the center but toward the end of the spore (Fig. 93). Elongation occurs with apparently little or no change in the location of the nucleus (Figs. 94 and 95). It should be emphasized that all the spores in one cyst are of one type with regard to the location and orientation of the nuclei. The different conditions observed do not seem to fit into a single pattern of development. This and other discrepancies observed suggest that two or more types of *Gregarina blattarum* may exist.

DISCUSSION OF CHROMOSOME BEHAVIOR IN GREGARINES

JAMESON (1920) and Naville (1931) have given complete historical accounts of the chromosome cycle in gregarines with critical discussions of the various phases. It would be superfluous to review at this time the same material in detail; but certain aspects of the chromosome cycle, upon which the present investigation has a direct bearing, may be profitably considered.

TYPES OF REDUCTION

Cephalina

According to Naville (1931), "L'étude du cycle chromosomique, des phénomènes réductionnels et de la fécondation des Cephalina est beaucoup moins avancée que celle des Acephalina. Pour aucune espèce nous ne possédons jusqu'à ce jour d'étude complète du cycle chromosomique telle qu'il en a été publié pour Monocystis par Mulsow et Naville, pour Diplocystis par Jameson et pour Urospora par Naville . . . . Chez les *Polycystidés* nous ne possédons que quelques documents fragmentaires."

Naville believes that the lack of information on the Cephalina is probably due to the difficulty of collecting the cysts in very great numbers, since they are expelled from the host soon after formation. By the methods used in the present studies, the difficulty of obtaining cysts of *Gregarina blattarum* in unlimited numbers, and at any desired stage of development, has been overcome; and the author believes that he has been able to demonstrate the details of meiosis for the first time in a

cephaline gregarine. Chakravarty (1935) recently made a study of *Hyalosporina cambolopsisae* Chakravarty, a cephaline form. Regarding meiosis in that gregarine he stated, "It is quite evident from the study of sections that the number of chromosomes is two and that the first division of the zygote nucleus is the meiotic division." Although the conclusion of Chakravarty may be justified on the basis of what he saw, his published observations and figures do not supply enough information for one to judge the correctness of the statement.

Early workers attempting to discover meiosis in cephaline gregarines have, as Jameson pointed out, concentrated their attention on the pregametic divisions. Several of them have clearly demonstrated an odd number of chromosomes in those stages. This is good a priori evidence of zygotic reduction; but clear and detailed descriptions of the process, based on actual observation, seem to be lacking. The author, therefore, agrees with Naville (1931) who stated that it is impossible at the present time to decide whether zygomeiosis is the rule in the Cephalina.

Acephalina

The chromosome cycle has been studied much more successfully in the Acephalina, and both gametic and zygotic meiosis are known to occur. Gametic meiosis was described in Monocystis by Mulsow (1911), Bastin (1919), Naville (1927a), and Calkins and Bowling (1926), and has been described in Urospora by Naville (1927). Zygotic meiosis was described in Diplocystis by Jameson (1920) and in Zygosoma by Noble (1938).

The work of Noble on Zygosoma, being perhaps the most conspicuous piece of work published on the chromosome cycle in gregarines since Naville's (1931) comprehensive review of the subject, requires particular attention here. In spite of Noble's unquestionably conscientious work, a careful study of his paper leads the present writer to feel that the material upon which Noble based his "sequence of changes immediately preceding and following the formation of the zygote" (most of the essential stages of the chromosome cycle) may have been in an advanced state of degeneration. The following observations are made in support of this view:

(1) "Out of approximately 150 cysts kept under various conditions in the laboratory, only one developed as far as the sporoblast stage." Apparently no other cyst in a late stage of development was observed. The wisdom of basing a number of important conclusions on one specimen in any case requires no comment, but when only one out of 150 cysts is not obviously in a stage of disintegration, that one certainly should arouse suspicion, and conclusions based on it cannot be very convincing. It is noted that Noble, himself, expressed some uncertainty as to whether that one cyst was entirely normal.

(2) The cyst studied contained all stages from gametes to spores with four nuclei. In normal cysts of *Gregarina blattarum* the rate of development is practically uniform throughout the cyst; obviously degenerate specimens often show an unequal rate of development. Although other workers have not been very specific on this point, one gains the impression that an essentially uniform rate of development within the cyst is common in gregarines.

(3) The nuclei of gametes, zygotes, and spores in many of Noble's figures are irregular masses of chromatin which have more the appearance of degenerating nuclei than of normal ones.

(4) Both the nucleus and cytoplasm in many of the stages represented are highly vacuolated. It is well known that vacuolization frequently accompanies degeneration.

(5) Noble observed, "The zygote nucleus does not divide until after the sporocyst membrane is fully formed." This is unusual; it suggests that the nucleus may have become inactive due to some abnormal condition and that the membrane simply continued its development for a time.

(6) The nucleus of the zygote "becomes dumbbell-shaped, and pinches in two." This behavior is very suggestive of a state of degeneration; for it seems inconceivable that a division which is regarded as meiotic can, at the same time, be amitotic.

(7) The nuclei of developing sporoblasts, when not vacuolated, are compact. This appearance was noted by the present writer in degenerating nuclei of *Gregarina blattarum* in which the normal nucleus is vesicular, ring-shaped or rod-shaped, depending on the stage.

(8) The spores were found to have only four nuclei rather than eight, which is common in gregarines. The most reasonable explanation is that development simply did not proceed any further.

(9) Some spores, which the author admitted to be abnormal, contained five nuclei rather than four. This point is highly significant in the light of experience with *Gregarina blattarum,* in which it was found that all the spores in a given cyst either develop in a normal manner or all degenerate. The presence of some admittedly abnormal spores in a cyst throws suspicion on other spores within the same cyst.

(10) The second metagamic division, like the first, appears to be by constriction. Here, again, the type of division seems to suggest an abnormal condition of the nucleus.

(11) Although none of these criticisms alone may be conclusive, all of them taken together seem to justify the belief that a renewed study of *Zygosoma globosum,* using more abundant material, might yield significantly different results.

In summarizing the types of reduction found in gregarines, it may be said that both zygotic and gametic meiosis are known to occur in the

Acephalina; and now direct and detailed evidence is produced to support the a priori belief that zygotic reduction occurs in some, at least, of the Cephalina.

Synapsis

In general, our knowledge of synapsis in gregarines is quite fragmentary. This may be due, at least in part, to the fact that synapsis seems to be common in the zygote; and early workers neglected this stage in their studies. More recent investigations have given us some definite information concerning both the haploid and the diploid forms.

Haploid Forms

Schellack (1912) mentioned synapsis in the zygote of *Gregarina ovata,* which is probably a haploid form, and apparently indicated the process in his figures, though he gave no detailed description. The process, as judged by the figures given, strikingly resembles that in *Gregarina blattarum,* since the chromosomes assume a polarized arrangement before karyogamy and maintain a similar arrangement during synapsis. A more detailed study of the chromosome behavior in the developing sporoblast of *Gregarina ovata* is much desired.

Jameson mentioned synapsis in *Diplocystis schneideri;* but the time at which it is said to occur seems rather unusual, as the following step by step study of the first metagamic division suggests. In the early stages of karyogamy, according to Jameson, "the two little clumps of chromatin granules are at first separate. . . . , but they later unite to form a large mulberry-like karyosome . . . . which contracts subsequently to form a more compact body. . . . ." This union of the two chromosome complements, immediately after fusion of the nuclei, and the subsequent "contraction" were not regarded as synapsis, although the present author notes that they occupy the same order in the sequence of changes as the phenomenon of synapsis in *Gregarina blattarum* and other haploid gregarines on which we have any information. Jameson further stated: "The karyosome commences to break up. Round particles are given off from it, which seem to move outwards along the achromatic strands towards the periphery of the nucleus." It is observed here that this process of outward movement corresponds, in the time sequence, to disjunction and the outward movement of the dyads in *Gregarina blattarum*. The next nuclear change in *Diplocystis schneideri* is a second contraction. Then the knot opens out. Jameson stated: "As the tangle becomes less obscure one can see that the spireme during this synapsis has become divided into six chromosomes." It was thus this second "contraction" which Jameson regarded as a process of synapsis. The present author observes that this "synapsis," being followed immediately by the anaphasic move-

ment, occupies the same position in the series of changes as the meta-
phase of ordinary mitosis and the "confused clump" metaphase in *Greg-
arina blattarum*. A careful and detailed comparison of the sequence of
nuclear changes in the zygote of *Diplocystis schneideri* with that in
Gregarina blattarum and with that in the auxocyte in metazoa thus leads
the present author to consider that the first "contraction" described by
Jameson may be, in reality, a process of synapsis, while the second "con-
traction" probably represents the metaphase.

Further information on synapsis has been given by Noble, who has
reported that in *Zygosoma globosum* "a process of synapsis immediately
follows fertilization." This, he believes, "is the first reported instance of
a definite synapsis in a nonseptate gregarine with zygotic reduction."

Finally, in *Gregarina blattarum* the two sets of chromosomes unite to
form three pairs immediately after the union of the two pronuclei. The
zygonemata have a polarized arrangement resembling that which is com-
mon in the auxocyte of metazoa. More information is thus added to our
meager knowledge of synapsis in the haploid gregarines.

Diploid Forms

Naville (1927) described in detail, and figured very clearly, synapsis
in *Urospora lagidis*. This, he remarked, "n'avait point été décrite jusqu'à
ce jour chez les Gregariniens." The zygote nucleus is at first vesicular
with peripheral chromatin and an endosome, no chromosomes being
recognized. Next there is a preleptotene stage, from which the chromo-
somes emerge in pairs. The paired condition is of rather long duration
and resembles synapsis in the auxocytes of metazoa. A slight difference
is noted here between *Urospora lagidis* and *Gregarina blattarum*. In the
latter the preleptotene changes occur in the pronuclei; and at the time of
karyogamy the leptotene threads are fully formed and ready to go into
synapsis. Thus, there is no stage in the synkaryon during which the
chromosomes are not recognizable.

In three species of Monocystis, Naville (1927a) did not find any
conclusive evidence of synapsis but supposed, by analogy with Urospora,
that the process probably follows immediately after fertilization. The
same author (1931) has also pointed out that the figures of Calkins and
Bowling (1926), representing the zygote of a species of Monocystis,
show the chromosomes rather definitely arranged in pairs.

The fact of particular interest with regard to synapsis in both the
haploid and the diploid gregarines is that this process always occurs, at
least in well known cases, in the nucleus of the zygote. Reduction in the
chromosome number, on the other hand, follows immediately after syn-
apsis in the zygote of the haploid forms (Gregarina, Diplocystis,

Zygosoma), while it is delayed until the process of gamete formation in the diploid gregarines (Urospora, Monocystis). Naville (1927, 1931) made the fascinating observation that the diploid gregarines, in which reduction alone is delayed, represent a condition intermediate between the haploid gregarines, which have both synapsis and reduction in the zygote, and the metazoa in which both processes are delayed until the time of gametogenesis.

These three types of chromosome cycles may be represented in tabular form as follows:

	Zygote		*Soma*		*Gamete*	
Haploid gregarines...2N	synapsis, meiosis	N			N	syngamy
Diploid gregarines...2N	synapsis	2N	meiosis		N	syngamy
Metazoa...........2N		2N	synapsis, meiosis		N	syngamy

Naville (1931) has expressed the entirely reasonable opinion that those forms with both synapsis and reduction in the zygote (Cephalina, certain Acephalina, Schizogregarinaria) represent a primitive condition, while the long delayed reduction in certain of the Acephalina is a more recent acquisition. If this opinion of Naville is correct, the implications with regard to the evolution of sex are obviously rather far-reaching. Possibly further study of the chromosome behavior in gregarines may contribute much more to our knowledge of the evolution of sex in the animal kingdom. Furthermore, if this difference in chromosome cycle is valid and fundamental, it may be a more natural basis for distinguishing the major groups of the gregarines than the presence or absence of a septum, the latter being merely a recent acquisition in certain haploid forms.

NUMBER OF MEIOTIC DIVISIONS

Haploid Forms

Previous workers have given us but little direct information concerning the number of divisions involved in the meiotic process in the haploid gregarines. Since, in the known forms, both synapsis and reduction are zygotic, one must admit that on theoretical grounds two mitoses may be necessary, if tetrads are formed, to accomplish both the disjunction of the homologous elements and the equational separation of their halves. Each of the two mitoses may in such cases, to use the words of Sharp, "be disjunctional for some elements and equational for others."

Schellack apparently observed synapsis and tetrad formation in *Gregarina ovata*. He did not, unfortunately, study subsequent changes. Further investigation of this form is highly desirable; but apparently, as Naville stated, two divisions are necessary to complete the reduction.

Jameson, who has given the most detailed description of the meta-

gamic divisions in a gregarine of this type, demonstrated numerical reduction in the first division and assumed the process of meiosis to be complete at that stage. Since synapsis and tetrad formation were not described, and since the second and third divisions were described very briefly, it is impossible to judge whether the second division is, in any sense, a meiotic division. Jameson, himself, was noncommittal on this question; but he gave no evidence to exclude the possibility, which theoretically exists, that meiosis may not be completed until the end of the second division. In *Zygosoma globosum,* Noble likewise postulated a numerical reduction in the chromosomes in the first metagamic division and gave the question no further consideration.

In the present paper, for the first time in gregarines, two meiotic divisions are described in *Gregarina blattarum.* Aside from theoretical considerations, certain definite, though admittedly inconclusive, observations seem to support the belief that the first two metagamic divisions should both be regarded as meiotic. Both synapsis and meiosis are zygotic, and tetrads seem to be formed in the prophase of the first division. If tetrads actually are formed, then two meiotic divisions may be a necessity. Chromosome number 3, during the first anaphase, frequently shows evidence that splitting has occurred at an early stage in the first division; this suggests that the first mitosis may be disjunctional for some elements and equational for others, in which case a second meiotic division is required to complete the separation of the maternal and the paternal elements. The chromosomes emerging from the first metaphase are larger than any seen elsewhere (except the tetrads); this is presumptive evidence of a bivalent nature and a further indication that equational splitting of the homologous chromosomes may occur in the early part of the first division. The prophase of the second division is characteristic of a second meiotic division, since the elements of the dyads become separated in that stage. In conclusion, it may be said that the series of nuclear changes in the first and second metagamic divisions of *Gregarina blattarum* appear strikingly similar, in all essential respects, to the meiotic divisions in metazoa. Further study on this and other haploid gregarines is necessary to confirm the apparent similarity; for, since the chromosomes are exceedingly small, certain of the questions involved can be positively answered only with the greatest difficulty.

Diploid Forms

In those gregarines with zygotic synapsis and gametic meiosis there is no apparent reason to suppose that more than one nuclear division is needed to complete the process of reduction; yet in some of these forms, at least, that division which accomplishes numerical reduction seems to

be followed by one or more equational divisions. Mulsow (1911) could not decide whether numerical reduction is followed by another division in Monocystis, while Calkins and Bowling thought that reduction occurs in the last pregametic division. Bastin (1919), on the other hand, believed that in *Monocystis agilis* Hesse the reduction is accomplished in two steps, as in the metazoa, although he was unable to observe the details. It is important to note that Bastin searched in vain for synapsis previous to the reduction division.

Naville (1927) seems to have clearly demonstrated a period of division following numerical reduction in *Urospora lagidis* (de Saint Joseph). The same process was found by Naville (1927a) in three species of Monocystis. He (1931) believed that Muslow and also Calkins and Bowling overlooked the last period of division. Thus, the occurrence of one or more mitoses following numerical reduction in the chromosomes may be the rule in the diploid gregarines. There is, however, no convincing evidence that these mitoses are involved in the meiotic process.

General Considerations

At this time certain general remarks may be made with regard to the chromosome cycle in gregarines:

(1) Since in the diploid forms meiosis is gametic and not immediately preceded by synapsis (the latter being zygotic in known instances), a single meiotic mitosis is sufficient to accomplish both numerical reduction of the chromosomes and the separation of the maternal and paternal elements.

(2) Any division following numerical reduction in these forms cannot, therefore, be regarded as being, in any sense, meiotic.

(3) In the haploid gregarines, on the other hand, synapsis and meiosis are both zygotic (insofar as we are able to judge at the present time). One must admit, therefore, that two mitoses may be necessary to accomplish both the disjunction of the homologous elements of the chromosome complement and the equational separation of their halves.

(4) Among previous workers only Jameson has given us anything approximating an adequate description of the second metagamic division in haploid gregarines; and he disregarded its possible role in meiosis.

(5) In *Gregarina blattarum* the metagamic divisions have been worked out in detail for the first time in a cephaline gregarine. The series of nuclear changes following syngamy appears to be similar, in all essential respects, to that found in maturation in metazoa. Detailed studies on other haploid forms are needed to confirm the opinion that meiosis is accomplished not in one division but in two, as in the metazoa.

(6) Finally, it is highly desirable that some method be devised for

identifying the chromosomes in the various stages, so that they can be individually followed through the cycle. A number of questions could thereby be positively answered. One might, for instance, determine definitely whether the two small chromosomes seen in the haploid nucleus in some gregarines actually belong to the same pair or to different pairs. This must still be regarded as an unanswered question and one of fundamental importance with regard to the pattern of the chromosome cycle. A dependable method of identifying the three chromosomes of *Gregarina blattarum* at all stages might lead, also, to an understanding of the many differences in the behavior of the short chromosomes and the long one. Further, the pattern of the chromosome cycle might be altogether different from that postulated in the present study or that known elsewhere among animals. At present, one must, admittedly, interpret the observed phenomena in a manner which seems most plausible in view of the facts known about chromosome behavior in other animals. One must, at the same time, admit that more precise data might lead to fundamentally different conclusions.

SUMMARY AND CONCLUSIONS

During the fall and winter of 1939 (September to the middle of December) 810 specimens of *Blatta orientalis* were examined for *Gregarina blattarum*. Only 5.3 per cent were found to be infected, and in each case the infection was light. At that time cysts were seen but rarely.

In January and February of 1940 about 30 per cent of a collection of roaches, which had been kept in the laboratory since the previous fall, were very heavily infected. Some of the cysts were fed to the roaches in an attempt to maintain a high incidence of infection, and others were used in these studies.

The process of encystment was observed a number of times after pairs of mature gamonts were placed in fresh undiluted egg albumen on a depression slide. The observations made on this process are in essential agreement with those made by Bütschli, but an attempt is made to explain why the newly formed cyst changes from a sphere to a prolate spheroid. The average ratio of the long to the short axis of fourteen cysts formed on a slide was found to be 1.76. Of 25 cysts formed in the same host from which the other material was obtained the average ratio was 1.22. These results indicate that the amount of restriction as to space during a certain critical period of encystment is an important factor in determining the shape of the cyst.

A scatter diagram shows a positive correlation between the long and short axes of a random sample of cysts indicating little or no tendency for the shape to vary with the size.

A histogram showing size distribution of cysts indicates that encystment seldom occurs until the gamonts have attained a certain definite minimum size.

The externally visible features of cyst development are described, and an explanation of sporoduct evertion is proposed. Neutral red and bromthymol blue indicate an acid reaction in the basal region of the sporoduct. Enzymes acting in an acid medium probably have a lytic effect on that portion of the cyst membrane which is in contact with the basal disc of the sporoduct. The membrane becomes weakened at that point, and the great pressure exerted on the cyst contents by the elastic membrane forces the sporoduct through the weakened area in the membrane.

Cysts kept until maturity in a moist chamber discharge their spores in very long chains. One continuous chain may contain as many as 10,000 spores. The chains of spores often become arranged in large coils containing many turns.

The mature spore is not truncate as described by previous workers; but it is covered by a mucoid sheath which gives it a truncate appearance. The sheath is adhesive and holds the spores together in the chain.

A detailed description of the nuclear changes during spore development is given. In the pregametic divisions three small chromosomes with a characteristic appearance are plainly seen. They are designated as numbers 1, 2, and 3.

The characteristic position assumed by the two gametes during syngamy and differences in the behavior of the pronuclei suggest physiological differences in the two copulating gametes. One of them is, therefore, designated as male and the other female.

A haploid set of three chromosomes is contributed to the synkaryon by each of the two pronuclei. The six chromosomes assume a characteristic polarized arrangement and undergo synapsis and tetrad formation. In the anaphase of the first metagamic division three dyads go to each daughter nucleus. The two elements of the dyads are then separated in the second metagamic division, resulting in four nuclei, each with a haploid complement of three chromosomes. It is thus seen that the zygote is the only diploid stage, all others being haploid.

The third metagamic division results in eight ring-shaped nuclei which transform themselves into long rods. These are the nuclei of the eight sporozoites.

Certain variations in the size of the cysts and discrepancies in the nuclear phenomena suggest that two or more varieties of *Gregarina blattarum* may be involved in these studies.

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PLATES

ALL DRAWINGS were made with the aid of an Abbe camera lucida. Figs. 1-20 were drawn from living material and are magnified approximately 60 times. Figs. 21-36 represent various methods and magnifications as indicated. Figs. 37-95 are from smear preparations, fixed and stained by methods indicated; they are magnified approximately 1850 times. Abbreviations are as follows: *S.*, Schaudinn; *Z.*, Zenker; *H.*, Heidenhain; *F.*, Feulgen; *G.*, Giemsa.

PLATE I

FIG. 1.—An unusually large sporadin; the only individual present in the host.

FIG. 2.—A trophozoite with epimerite and three pairs of very small gamonts in syzygy. The latter show that pairing may occur in very immature individuals.

FIG. 3.—A rather rare instance of multiple association.

FIGS. 4-11.—Successive stages in the process of encystment, as seen in one pair.

FIG. 4.—Beginning of encystment.

FIG. 5.—About 15 minutes later. Opposite ends are brought together.

FIG. 6.—About 10 minutes later. The two individuals are more closely associated.

FIG. 7.—About 5 minutes later. The two individuals appear to be firmly cemented together.

FIG. 8.—About 15 minutes later. A cyst membrane is being secreted; the young cyst is almost a perfect sphere.

FIG. 9.—About 15 minutes later. The cyst rather suddenly begins to elongate.

FIG. 10.—About 15 minutes later. The cyst is still in the process of elongation and the membrane is thicker.

FIG. 11.—About 1 hour later. The cyst is complete; but the membrane is abnormally thick at the ends, since rotation of the individuals within is inhibited by excessive elongation.
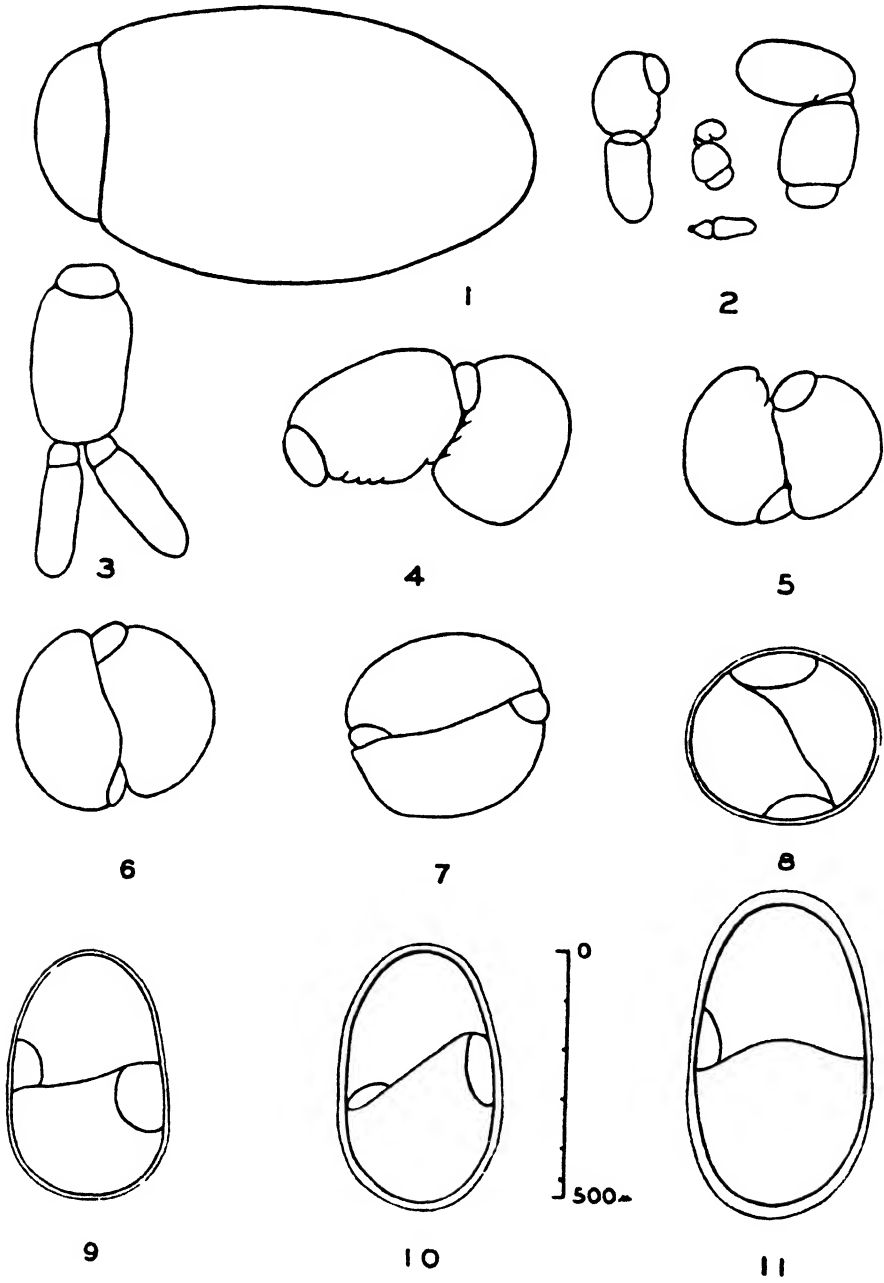
PLATE I

PLATE II

Fig. 12.—A cyst formed by three individuals of different size.

Fig. 13.—An unusually small cyst.

Fig. 14.—An unusually large cyst.

Fig. 15.—A cyst formed by two individuals of very unequal size.

Figs. 16-20.—A number of successive developmental stages, as observed in a single cyst.

Fig. 16.—The cyst as it appeared after the gametes formed on the periphery.

Fig. 17.—About 30 minutes later. The gametes are seen to be separating from the residual mass.

Fig. 18.—About 20 minutes later. All the gametes have broken off and are floating freely in a liquid zone around the periphery. The two residual masses flow together.

Fig. 19.—About 10 minutes later. The residual masses are completely fused. The clear peripheral area containing gametes is still present.

Fig. 20.—About an hour later. The clear area disappears, and the contents appear uniformly granular.

12 13 14 15 16 17 18 19 20
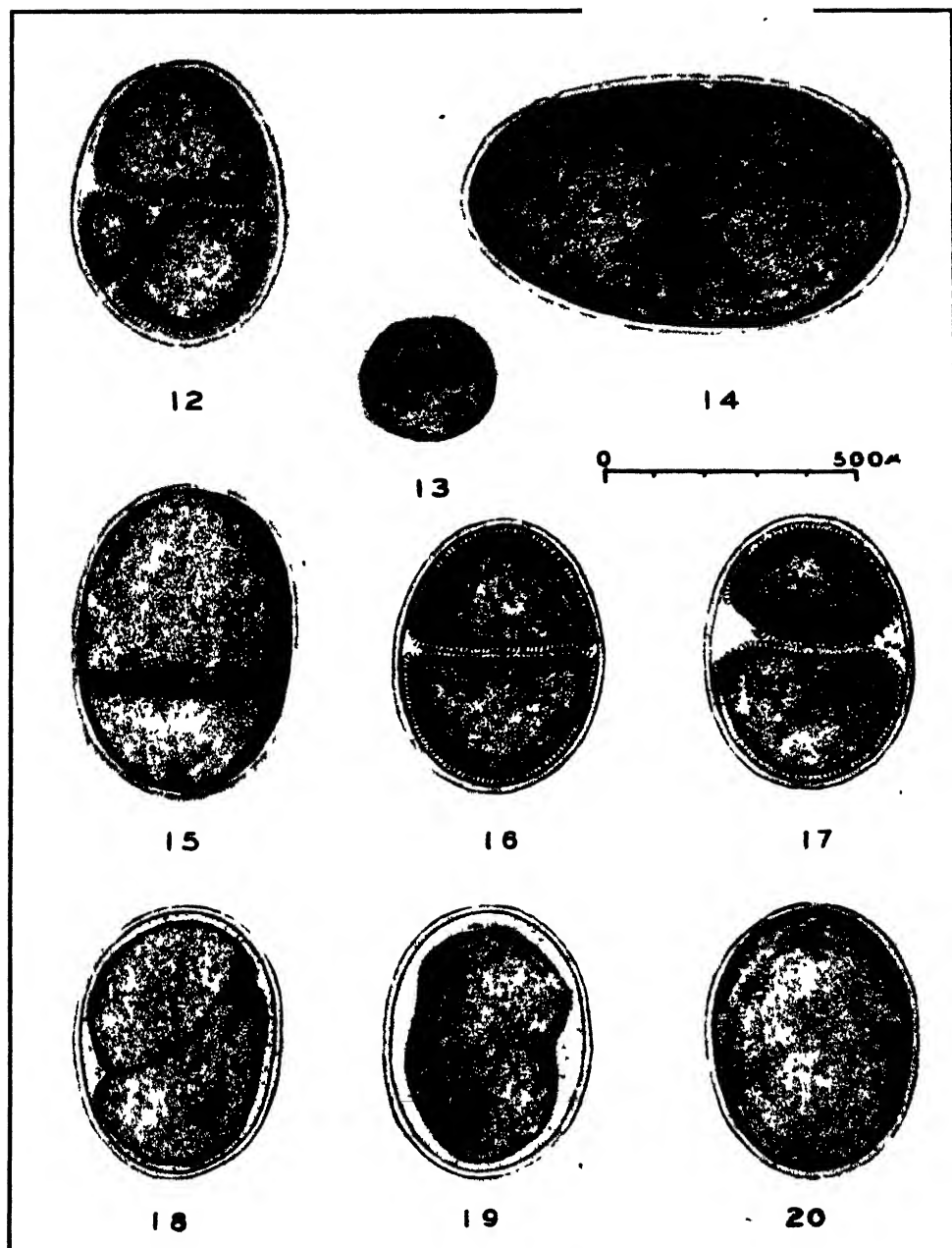
PLATE II

PLATE III

Fɪɢ. 21.—Surface view of the basal disc of a sporoduct before the evertion of the latter. In life. × 413.

Fɪɢ. 22.—Optical section of a sporoduct showing expulsion of spores. In life. × 413.

Fɪɢ. 23.—Side view of basal disc just before evertion of the sporoduct. The basal disc is making its way through the cyst membrane and is elevated above the surrounding area. In life. × 94.

Fɪɢ. 24.—An incompletely everted sporoduct after the spores have been expelled through other sporoducts. A cavity in the cyst membrane due to lytic action in the region of the basal disc is shown. Neutral red. × 413.

Fɪɢ. 25.—An everted sporoduct. The basal region of the sporoduct and certain granules within the cyst are heavily stained with neutral red. × 413.

Fɪɢs. 26-27.—Two optical sections of the same cyst membrane before and after the cyst was ruptured; showing great thickness and laminated appearance of the membrane after the cyst contents have escaped. In life. × 413.

Fɪɢ. 28.—A short chain of spores, showing how they are cemented together. In life. × 1730.

Fɪɢ. 29.—Optical section of a spore showing a mucoid sheath covering the true spore membrane. In life. × 1730.

Fɪɢ. 30.—A fresh spore with the mucoid sheath removed by acetic acid. × 1730.

Erratum: The scale above Figs. 29 and 30 represents 10 μ instead of 20 μ.
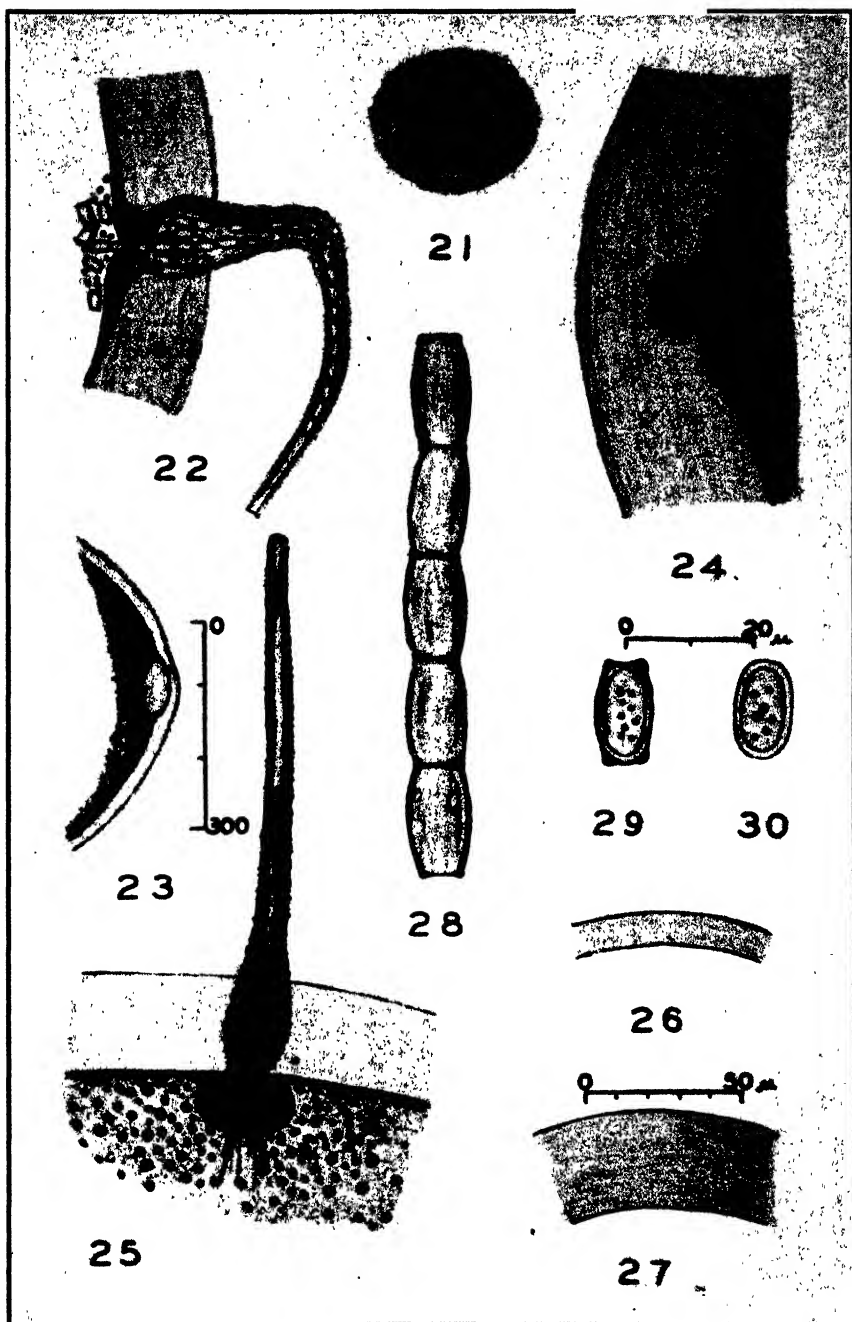
PLATE III

PLATE IV

FIG. 31.—Photomicrograph of a cyst and discharged spores; showing extreme length of a single spore chain. In life. × 48.

FIG. 32.—Photomicrograph of a normal cyst a few hours before discharge of the spores. In life. × 48.

FIG. 33.—Photomicrograph of the same cyst the next day when the spores were discharged; showing great decrease in size due to contraction of the elastic cyst membrane. In life. × 48.

FIG. 34.—Photomicrograph of spore chain enlarged to show individual spores. In life. × 470.

FIG. 35.—Photomicrograph of mature cysts developed in a moist chamber. The chains of spores are arranged in large coils. In life. × 48.

FIG. 36.—Photomicrograph showing spores suspended on the surface film of an air bubble, indicating the presence of oily substance on the spores. In life. × 140.
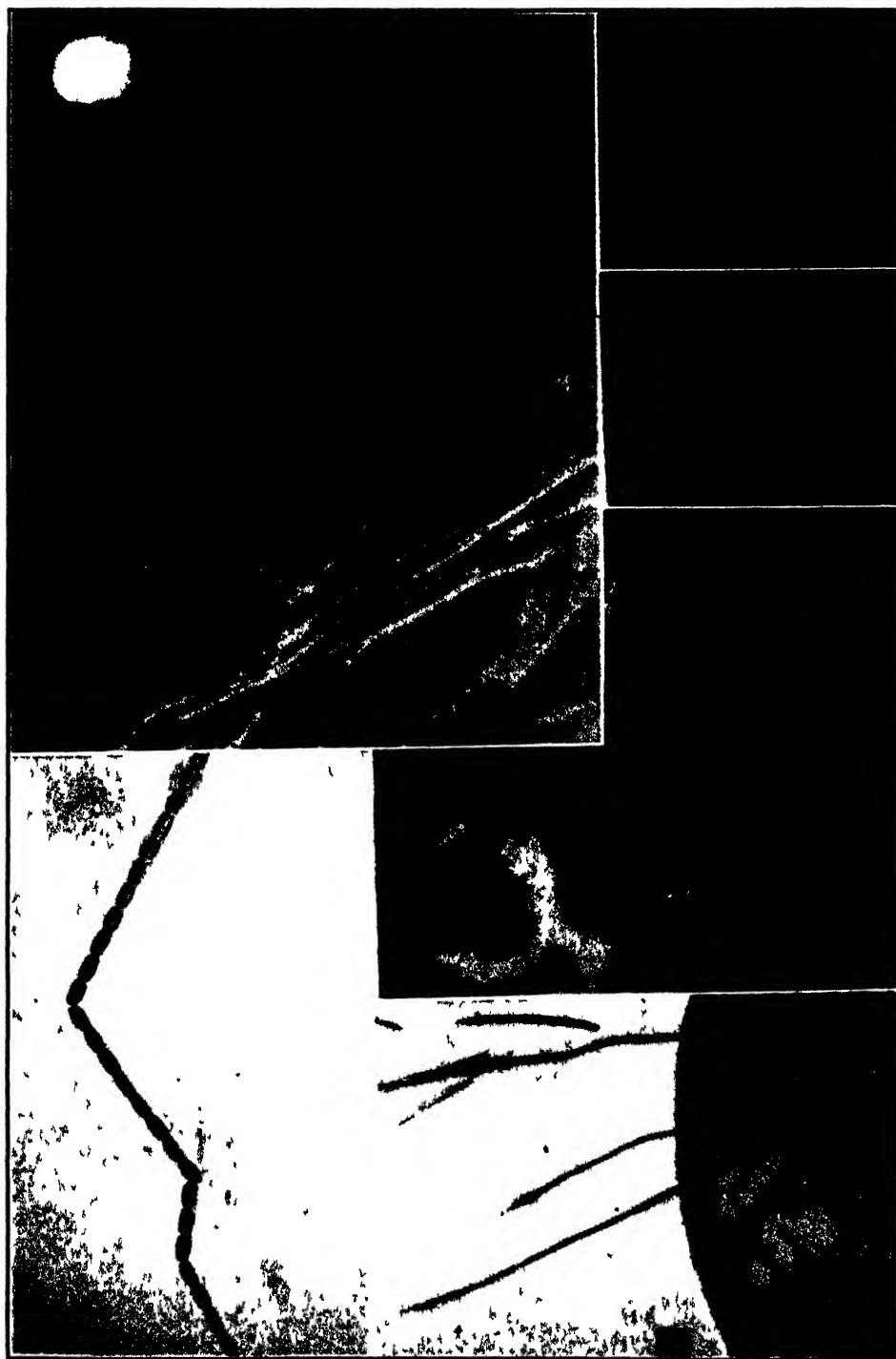
PLATE IV

PLATE V

FIG. 37.—Anaphase in a pregametic division, showing three chromosomes which are characteristic in size and arrangement. The two short ones are 1 and 2, the long one is 3. S.-F.

FIG. 38.—Later anaphase. S.-F.

FIG. 39.—A telophase. S.-F.

FIG. 40.—Interphase or early prophase. S.-F.

FIG. 41.—Interphase and prophase nuclei. S.-F.

FIG. 42.—A number of gametes just before they separate from the parent mass. S.-G.

FIG. 43.—Gametes becoming rounded shortly after separating from the parent mass. S.-H.

FIG. 44.—Two gametes after a period of growth; showing perinuclear vesicle. S.-H.

FIG. 45.—Early stage in syngamy; showing characteristic manner in which the gametes come together. S.-H.

FIG. 46.—Later stage in syngamy. The perinuclear vesicles have fused into one which contains the two pronuclei. S.-H.

FIG. 47.—Later stage. The nuclear membrane of the posterior pronucleus has broken down and three chromosomes have emerged. Three prophase chromosomes are distinguishable in the other. Z.-H.

FIGS. 48-49.—Peculiar appearance during syngamy in certain cysts. These are not in series with the other figures. S.-F.

FIG. 50.—Later stage in syngamy; showing the chromosomes of the anterior pronucleus in the unravelling stage. With the breakdown of the nuclear membrane of the anterior pronucleus, the membrane of the common perinuclear vesicle becomes the membrane of the synkaryon. Z.-H.

FIG. 51.—The two sets of 3 chromosomes from the two pronuclei lying side by side in the leptotene stage. Z.-H.

FIG. 52.—Zygote showing 6 polarized leptotene threads in the synkaryon. Z.-H.

FIG. 53.—Pairing of homologous chromosomes. The zygotene stage. Z.-H.

FIG. 54.—The pachytene stage. The chromosomes are much shorter and thicker. Chromosome 3 (?) characteristically thicker than the others. S.-H.

FIG. 55.—A stage in tetrad formation. The chromosomes are still shorter and thicker and are no longer polarized. S.-H.

FIG. 56.—Three tetrads lying on the periphery of the nucleus. Z.-H.

FIGS. 57-58.—Showing precocious disjunction in tetrads 1 and 2 while the nuclear membrane is still intact. Z.-H.

FIG. 59.—Metaphase. The chromosomes are characteristically clumped together. Z.-H.

FIG. 60.—A slightly later metaphase. Dyads 1 and 2 lie side by side while tetrad 3 is V-shaped. S.-H.

FIG. 61.—Early anaphase. S.-H.

FIG. 62.—Later anaphase showing disjunction in 3. S.-H.

FIG. 63.—Anaphase. The tendency for the elements of the dyads to separate along the equational plane is seen during disjunction in 3. S.-H.

FIGS. 64-65.—Later anaphase stages. A thread connects dyads 3. S.-H.
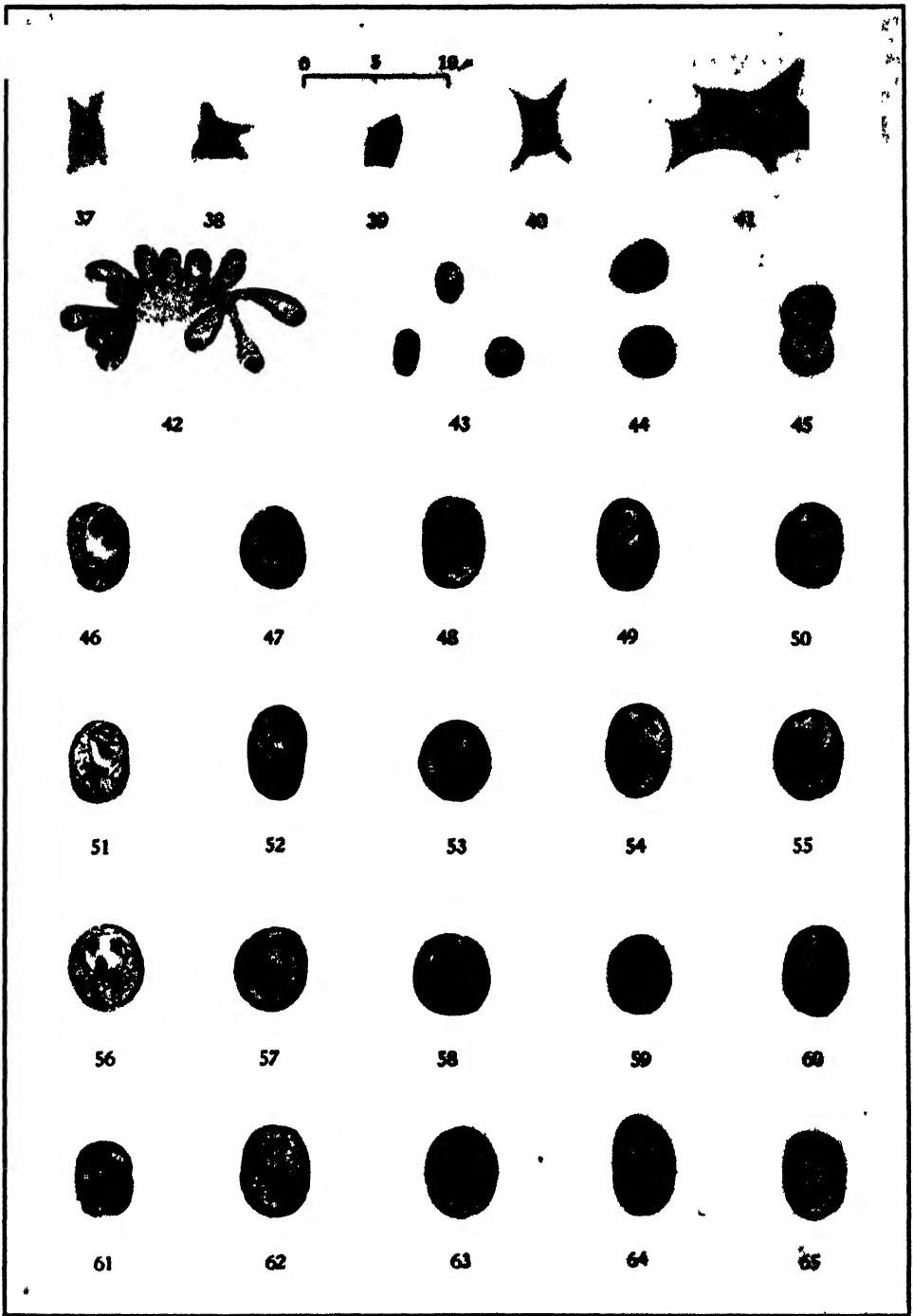
PLATE V

PLATE VI

FIG. 66.—Early telophase. S.-H.

FIG. 67.—Later telophase. S.-H.

FIG. 68.—Interphase. The nucleus is vesicular with chromatin granules scattered on a fine reticulum. This stage marks the end of the first metagamic (first meiotic) division. S.-H.

FIG. 69.—Prophase of second metagamic (second meiotic) division. Separation of the two elements in the dyads is seen to have occurred. S.-H.

FIGS. 70-71.—Metaphase (?). Long thin chromosomes lie in confused masses. S.-F. and Z.-H. respectively.

FIG. 72.—Metaphase in which the chromosomes are short and thick and lying in a clump. Z.-H.

FIGS. 73-74.—Anaphase stages. S.-F.

FIG. 75.—Early telophase. The chromosomes fuse to form an angle. S.-F.

FIG. 76.—Later telophase. The angles bend into circles which transform into vesicular nuclei. S.-F.

FIG. 77.—Interphase after second metagamic (second meiotic) division. The meiotic phenomena are now complete and each nucleus has a haploid set (three) of chromosomes. S.-F.

FIG. 78.—Prophase of the third metagamic division. Z.-H.

FIGS. 79-80.—Later prophases. The three chromosomes come to lie parallel with one another. S.-F.

FIG. 81.—Metaphase. The chromosomes lie in confused clumps. S.-F.

FIGS. 82-84.—Anaphase stages. S.-F.

FIG. 85.—Early telophase. The three chromosomes in each nucleus fuse into an angle. S.-F.

FIGS. 86-88.—Later telophase stages. The nuclei become circles. S.-F.

FIG. 89.—Each nuclear ring contains two granules, a large inner one and a small outer one. S.-F.

FIG. 90.—The nuclear rings elongate. S.-H.

FIGS. 91-92.—The final nuclear change is a transformation of the nuclear rings into long rods enlarged at the ends. S.-F.

FIGS. 93-95.—Sometimes the nuclei lie at or near the center of the spore, in which case the inner chromatin granule is small and the outer one is large.
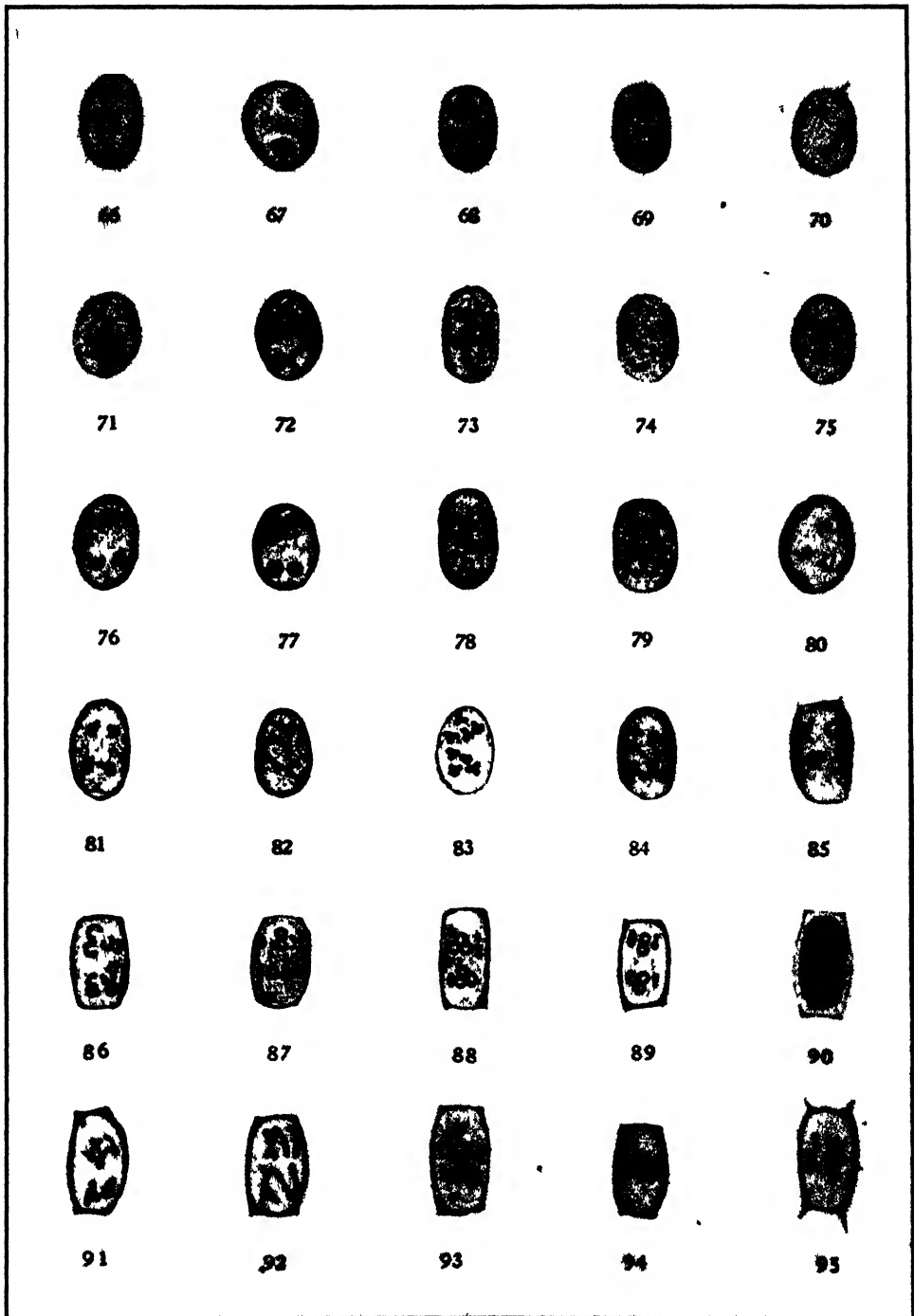
PLATE VI

ILLINOIS BIOLOGICAL MONOGRAPHS

Vol. XVIII   No. 3

EDITORIAL COMMITTEE

TERRITORIAL AND MATING BEHAVIOR
OF THE HOUSE WREN

WITH 32 FIGURES

BY

S. CHARLES KENDEIGH

CONTENTS

ACKNOWLEDGMENT

I. INTRODUCTION

THE REQUIREMENTS and behavior of the house wren, *Troglodytes aedon,* in respect to territory are similar to those described by Howard (1920, 1929) for several passerine species. In the following discussion it will be apparent how the behavior of the house wren (Fig. 1) satisfies the definition given by Howard (1929, p. 63) that "when territory is imperative, a male isolates himself, makes himself conspicuous, becomes intolerant of other males, and exercises dominion over a definite area." Territory is generally considered as important in various ways: as a means by which birds become paired and mated, as an insurance of adequate nest-sites and food supply for adults and young, and as a safeguard against disturbance. The process of courtship and mating can scarcely be separated in the house wren from the phenomena of territory, as they are so vitally interwoven and intrinsically related.

There is considerable literature on the life-history and behavior of the house wren. A bibliography including every mention of information dealing with territory, mating, interrelations, and nesting in this species would run into dozens of references. As very few of them tend to tell the whole story, citations will be made only when they have a direct bearing on topics considered in the following pages, although for a general background the following references may be consulted: Wright (1909), Baldwin (1921), Sherman (1925), and Allen (1927). Likewise the study of territory in the St. Kilda wren, *Troglodytes t. hirtensis,* by Harrisson and Buchan (1934) has a direct relation, as does the recent life-history study of the European wren, *Troglodytes t. troglodytes,* by Kluijver *et al* (1940). References for comparative purposes will be made to these wrens and to the long-billed marsh wren, *Telmatodytes palustris,* that was studied by Welter (1935), but otherwise no attempt will be made at a monographic treatment of territorial and mating behavior as it applies to birds in general.

Since this paper was written, an article by Miller (1941) dealing with the Bewick wren, *Thryomanes bewickii,* has appeared. Items in the behavior of this wren of special interest for comparison with the other members of this family discussed in the following pages are here briefly summarized. This species of the southern United States has several subspecies, some being migratory, as *T. b. bewickii,* but others, as *T. b. spilurus* in California, which received major attention, being permanent residents. The latter, at least some more mature individuals, maintain a territory throughout the year, although less vigorously during the winter. Defense of territory appears to be entirely by song. Only the male sings, and the singing period lasts from early spring to late autumn. The female

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takes no part in the territorial relations, although she appears to be cognizant of the boundaries of the territory belonging to her mate and does not venture outside. The territories average about an acre (0.4 hectare) in size. Mating occurs in early spring; the sexual status of paired birds frequently observed in winter is uncertain. Individuals recognize each other's sex by differences in call-notes and by the male's song. The female has special notes that serve as an invitation to the male for copulation. Two broods are raised during the season. Both sexes share in nest-building; the nests are placed in tree cavities; and pieces of snake skin are often incorporated in the nest-material. Although the male may start several nests, the possession of multiple nests is not a characteristic trait of this species as in some other members of this family. Although the male does not incubate, he is closely attentive, frequently feeding the female on the nest or elsewhere and sharing in the care of the young.

The study here reported covers the nineteen-year period from 1921 to 1939, inclusive, at the Baldwin Bird Research Laboratory, near Cleveland, Ohio. Perhaps the study actually began considerably earlier, for in Dr. S. Prentiss Baldwin's 1919 paper on the "marriage relations of the house wren," in which he reported on studies initiated in 1914, he tells how male birds sing and begin nest-building and compete with other males for the possession of nest-sites. Dr. Baldwin often stated that his notes were "full of territory," yet their significance as such did not appear until he had read Howard's classic study in 1920. Since 1921, detailed observations are available and are here summarized on the territorial behavior of 142 male and 147 female birds. Since many of these birds returned to the area year after year or had two broods in the same year, altogether some 331 matings between males and females are recorded, each mating the climax and goal of an individual territorial maneuver. This is the nineteen-year population on the "Hillcrest" area (Fig. 2). Altogether, the history of 215 individual male territories enter into this study. Many observations made in the "Outfield" area are also included as they bear on particular points.

The Hillcrest area (Fig. 3) included the fifteen acres immediately around the former home of Dr. and Mrs. Baldwin and at the top of the west bluff of the Chagrin River Valley. On the north the study area merged into hard maple-beech woods that extended fairly continuously for several miles beyond. The boundary on the east contacted several acres of cultivated land and pasture transversed by a wild rose lane and scattered trees and shrubs. Another estate of similar composition lay to the south, and extensive shrubby pastures adjoined to the west.

On the fifteen acres (six hectares) of the Hillcrest area itself, besides several buildings and long driveways, there were flower and vegetable
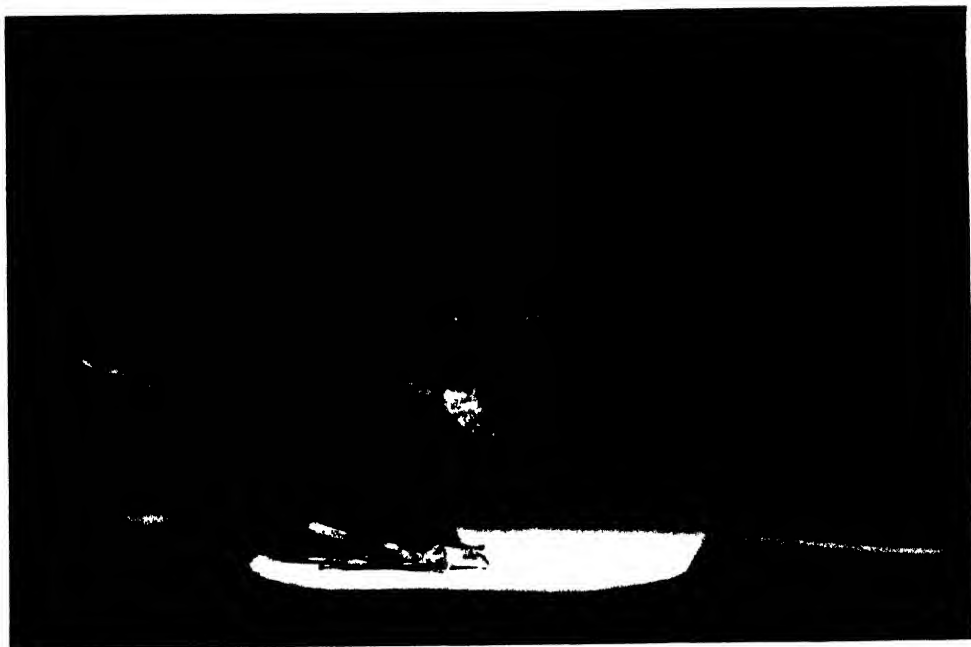
Fig. 1.—House wren standing on trap-door perch at nest-box.
Note the celluloid band around the right leg of the bird.

Fig. 2.—Air-view of Hillcrest area looking west. Mayfield Road on the left marks the south boundary, and West Hill Drive, extending to the right near the top, marks the west boundary. The fence in the lower right corner is the eastern limit of the area. The hard maple grove is in the upper right corner. The barns and north edge of the area are not shown. Other features of the area may be identified from Fig. 3.
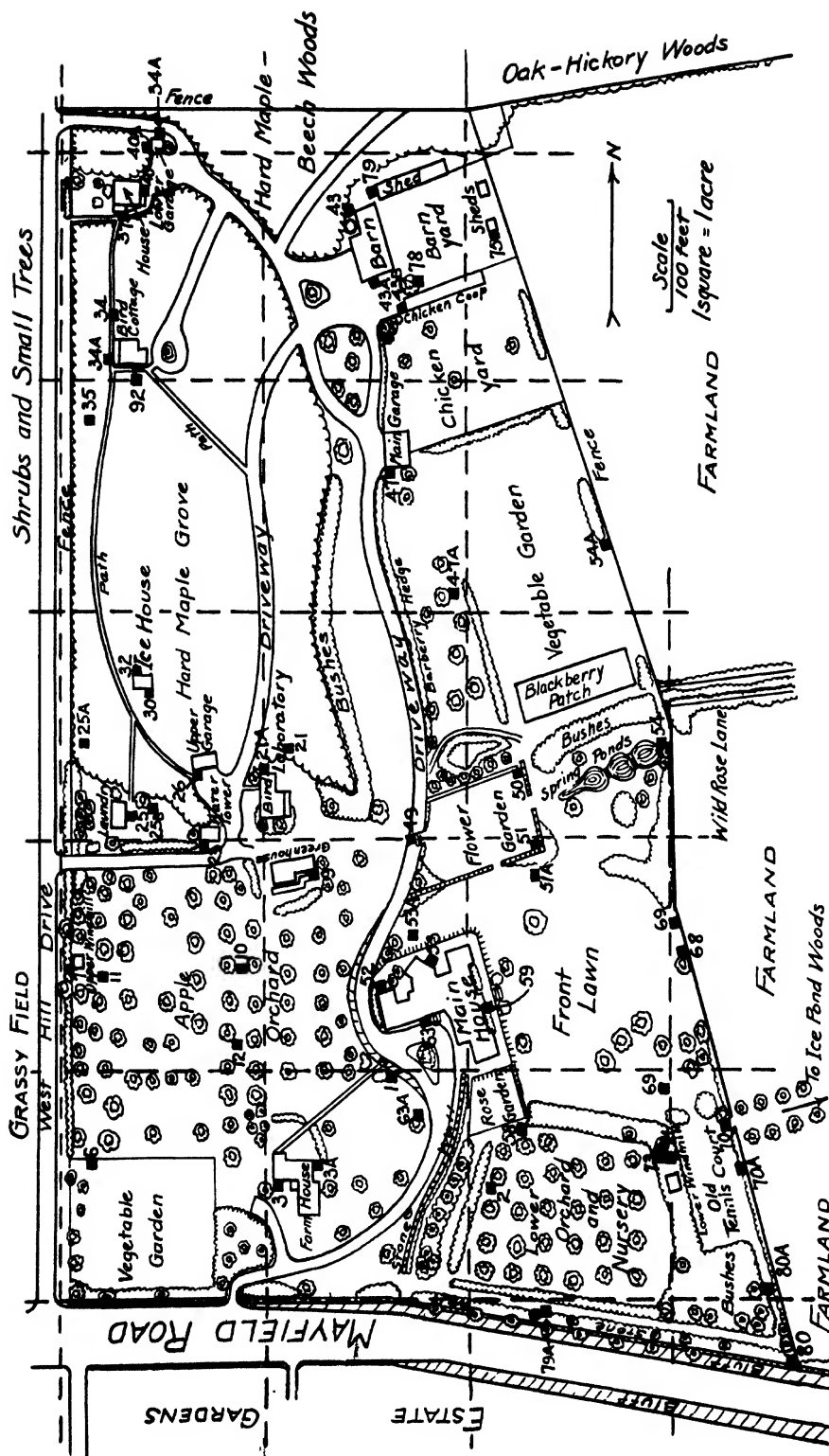
FIG. 3.—Generalized map of Hillcrest area, showing location of all boxes (numbered squares) used by house wrens from 1921 to 1939, inclusive. Minor changes from year to year in landscape and buildings are not indicated. Likewise slight changes in location of boxes are not shown here, although they are indicated on the year-by-year maps. The grid of squares, each equaling one acre, is for more accurate reference to this base map of the territories shown in the simplified maps, Figs. 7-32.

gardens, orchards, extensive lawns, a grove of tall hard maples with thick undergrowth, and many shade trees and cultivated shrubs of great variety. It was really a man-made forest-edge type of habitat, ideally favorable for the nesting of the house wren. Some forty boxes suitable for nesting were available, many more than were needed or ever used at any one time. These boxes were essentially permanent in location, as changes from year to year were slight. Rarely indeed did the wrens ever attempt to nest in natural cavities. In spite of abundance of nest-sites, strife between birds for possession of particular boxes was common. How behavior would be modified in areas where only natural nest-sites were available, needs to be studied, but doubtlessly the fundamental behavior would be the same.

The Outfield area (Fig. 4) included the Gates Mills village and vicinity. Its dimensions were approximately one and a half miles (2.4 kilometers) north and south, and one mile (1.6 kilometers) east and west. Hillcrest Farm lay near the center of this area, and the village itself lay in a deep valley, 300 feet below the surrounding upland. Much of the area was wooded, especially on the bluffs and to the north of Hillcrest. The western part of the area mapped was largely barren shrubby pastures of poor wren habitat and did not enter extensively into the study, the majority of the nest-boxes being in the southern and eastern parts. Work in the Outfield was started in 1926 (Baldwin and Bowen, 1928) and continued until 1938, although in decreasing amounts during the later years. During the period of main effort approximately 300 boxes were operated on some 70 different estates. An attempt was made to visit each box once a week, but some boxes were visited more frequently; others, only a couple of times each season. Record was made on each visit of progress of nesting, and a special effort was made to capture and band all adults and young. Identification of the entire wren population in the area was attempted. Where birds were found nesting in natural cavities, the nests were often transferred to boxes erected nearby so that the wrens could be caught and banded and their activities followed more easily. The purpose of this extensive study in the Outfield was to follow the movements of individual birds and to obtain ample data on mating and on nesting life.

For identification purposes the birds were trapped at their nest-boxes and banded with numbered government aluminum bands. The trapping was easily done by means of a movable perch that could, by means of a string, be closed over the entrance hole of the box after the bird had entered (Fig. 1). The bird was then induced to leave the box and enter a gathering net held over the entrance hole so that it could be more easily handled. During the early years of study, both adult birds were sometimes caught at about the same time or before they had become thoroughly
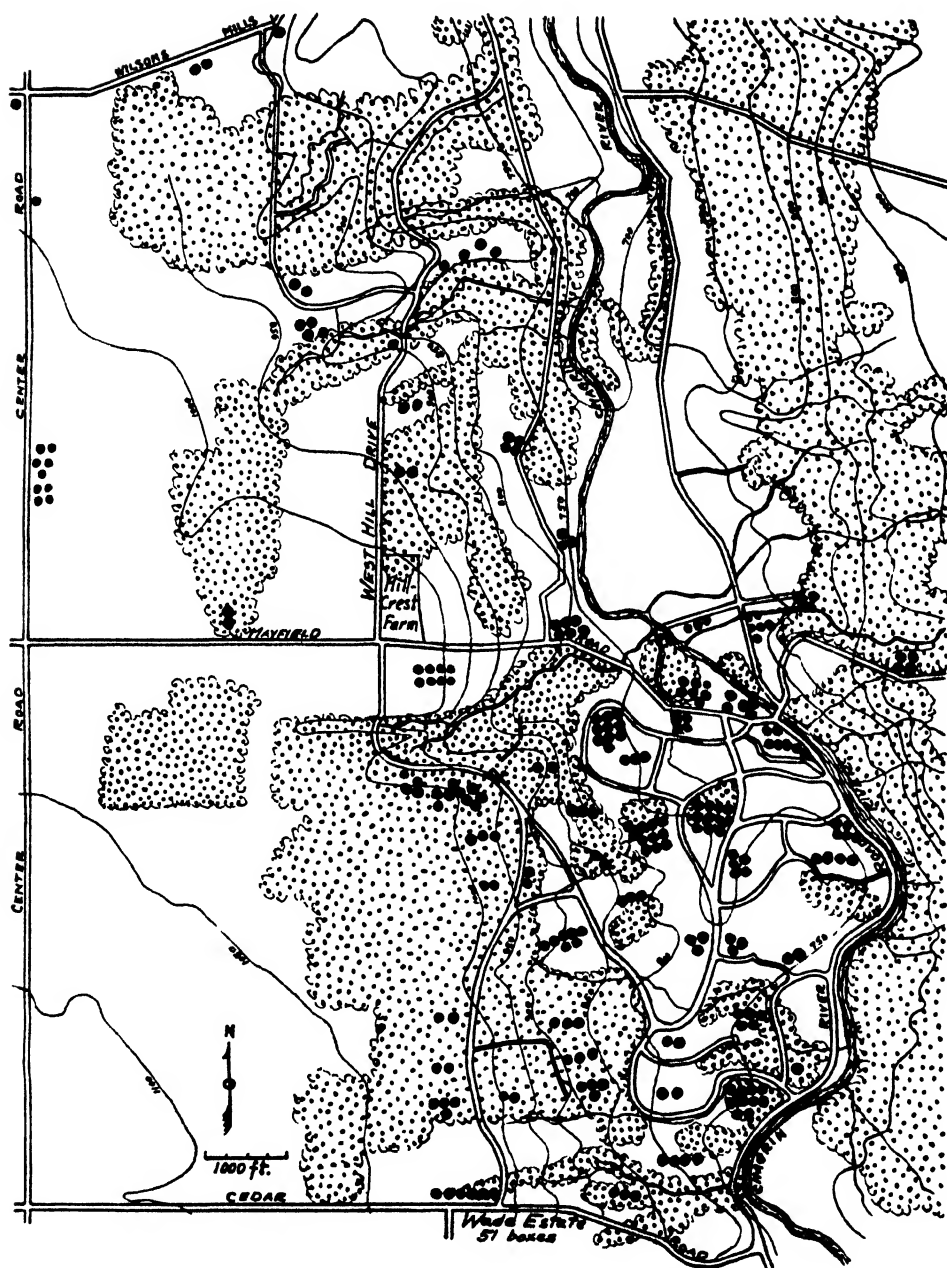
FIG. 4.—Map of the Outfield area, showing location of boxes by large dots. Contour lines are indicated. Stippled areas mark the location of forests or thick stands of trees. Areas not stippled are farmland and village. Gates Mills village lies mostly in the network of curving roads west of the river between Mayfield and Cedar roads.

established in nesting, so that disturbance of normal territorial behavior undoubtedly entered in to some extent and accounted for some undue shifting of birds from place to place. In later years the adult birds were not caught until the young had hatched and then usually on different days, so desertions were less common. Since the two sexes appear identical in the field and are separable only by behavior and by the male's song, colored celluloid bands for sex recognition were used as early as 1925, and consistently thereafter. In the hand, the sexes could quickly be distinguished during the breeding season by the presence of a brood patch only in the female. The sex bands were placed around the other leg than that which held the aluminum band (Fig. 1). Red was used for male and yellow for female. Usually the presence or absence of the sex band in connection with the location where observed gave also recognition of the bird as an individual. When a returning bird had been banded as a nestling, its age, of course, was accurately known. In an earlier paper (Kendeigh and Baldwin, 1937, p. 115) it was demonstrated that young birds are much more prone to wander into new regions than are adults, where the tendency to return in subsequent years to or near the place where they had previously nested is almost universal. All new unbanded birds of both sexes coming into the area were, therefore, considered birds in their first breeding season and to have hatched the preceding year or, rarely, two years before. Certainly this criterion is open to occasional exceptions, but it permitted logical explanations of various behavior phenomenon which otherwise would have remained obscure. This point is further considered on pages 17-19.

Since territory in this species is not large and since the adult birds return to their nest-box every few minutes, the limits of the territory and changes in its boundary were easily determined by observation. We were on the Hillcrest area daily from early June to September and less frequently through May and April. To visualize the dynamics of territorial behavior, a detailed map of the area was pinned on the laboratory wall. This map showed precise location of buildings, gardens, trees, and shrubs (Fig. 3). The territorial boundaries were marked, and changes through the season were followed as carefully as possible.

Nesting commonly began in early May and continued to middle or late August. This is the "breeding season" referred to in the following pages. The season is divided conveniently into two "breeding periods." The "first breeding period" terminates in late June when the majority of first broods are well on their way toward being independent individuals. The "second breeding period" begins in late June or early July and lasts to the end of the season. This is the period of second broods for those birds that nest twice. Not a few individuals, however, may nest for the first time in this second breeding period. These two periods are not

sharply distinct. Late arriving individuals may not start to nest until early or middle June, so that their first broods are not completed until the second breeding period is far along. Such a division is further complicated by birds starting again after the destruction of an early nest. However, the majority of nesting attempts fit in well with these two periods, and this division facilitates the analysis of territorial and mating relations. Within each period, nest-building by the female involves a period of 2-3 days, one egg is laid each day during the egg-laying period until the full complement of five to seven eggs is completed, and incubation lasts about 13 days. The young birds, after hatching, are cared for in the nest for 15 days, and after the young fly from the nest, their care by the parents continues for another 13 days, or until they become entirely independent.

For illustrating and supporting the various points brought out in the discussion and to put into available form for future reference or study of topics not here considered, case histories of each individual territory have been compiled (Section VIII). The identity of the male and female on each territory is given so far as it is known. The band number of the bird is given without parenthesis after the sex, both in the case histories and throughout the text. For the sake of completeness, work done from 1914 through 1920 is also indicated. Dr. Baldwin's notes first became complete and the study of house wren behavior took a serious form in 1921, so that beginning with that year, each territory is given a number. Maps were not made of the territories until 1925. During the early years, the boundaries of each territory were indicated during the progress of each summer's observations by means of pins and thread, and usually only the greatest extension of these boundaries were permanently recorded at the end of the season. During later years the territorial boundaries were marked in pencil and dated so that changes during the season would be permanently recorded. Thus the maps that are here reproduced (Figs. 7-32) show greater detail as the years progress. The history of each bird that returned one or more years is also compiled (Table 5), so that by cross-reference to the territorial accounts a complete story for each bird may be worked out for its entire life.

II. SPRING ARRIVAL OF BIRDS

THE FIRST males that arrive on the area in early May are in song immediately. Occasionally at this time a bird may be observed moving through the Hillcrest area, not singing and keeping well hidden in the bushes, but most of the migrating individuals probably move northward through the Chagrin River Valley, 250 feet below. It is our impression, based on movements of newly arrived birds, that they have come up from lower down in the valley, frequently entering the study area (Fig. 3) at

the southeast corner and then spreading fanwise to the boxes that they select. A less common but regular point of entry is the northeast corner. The southwest and west sides are bordered by open fields, and while they contain scattered shrubs and clumps of briars they seem not to be important migration paths. The first males to come have the choice of territories. Most popular seem to be the areas around box 25 and around box 47; after that perhaps around boxes 37, 74, and 53, and then boxes 43A, 59, 3, and 49.

Integration of the Breeding Population.—To give a better conception of the manner of first appearance and building up of a season's wren population, let us consider the year 1933 (Fig. 19). The first wren, a male, probably C68910, a return bird from the preceding year, was seen in the bushes by the laundry (Fig. 3) on April 14, the earliest record we have for any year. He was singing to some extent and scolding. Later he was down near the laboratory and established territory No. 129. The next day, another male, probably F45946, also a return, was singing near the garage; he later established territory No. 130. The following day, a third male, probably H18577, appeared around the main house; he later laid ownership to territory No. 125. This bird as well as all others not indicated as returns were very likely first-year birds. No new birds arrived for ten days. On April 26, an unidentified male was in the ice pond woods. On April 27, male, H18582, came to the laundry and established territory No. 128. On the 28th, a non-singing bird was seen in the bushes east of the barns, possibly a migrant or possibly a female, as the first female, H18566, came in on April 29 and inspected boxes 21A, 21, and 49 (129). The same day a new male, unidentified, was at box 80 (131).* On April 30, male, H18570, began setting up territory No. 132 near box 74. Another slack period ensued, although a return male, F58648, came to box 40A (136) and female, F58248, came to box 49 (129) some time during the first nine days of May. On May 12, two males arrived, H18588 at box 72 (133) and F45987, a return, at box 54A (134), and one female, F45942, a return, who went to box 25 (128). On May 16, an unidentified female came to box 80 (131), and about this time female, F58493, was at box 70 (132). On May 20, three more males came in, H18580 at box 10 (126), H18600 at box 11 (127), and L24102 at box 43 (135), and also three females, H18583 to box 10 (126), F58955 to box 11 (127), and H18587 to box 54A (134). It is quite possible that these six birds migrated more or less together. The last two females arrived on May 24, H18581 going to box 63 (125) and H18584 to box 43 (136).

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*Numbers in parenthesis following box numbers and not otherwise identified refer to history of individual territories; see Section VIII.

Although the actual date of arrival in the area could not always be determined with certainty, the time for beginning of nesting activities was approximately determined in 186 instances for males and 165 instances for females for the period 1921 to 1938 inclusive. The median date for *all* the males to begin nesting activities is May 11, although the median date for the *first* male activity is May 1, and for the *latest* male to begin activity, at least on Hillcrest, is June 22. Females average later, the corresponding three dates being May 20, May 11, and July 1. When the first activity of males and females is analyzed respective to age and combined into half-month intervals, the results shown in Fig. 5 are obtained. Although for the season as a whole, records for first-year males were 1.5 times as numerous and for first-year females 3.2 times as numerous as for older birds, as many old males as first-year males arrived between middle April and middle May, and there were almost as many older females as younger ones. From middle May to middle June the picture is different. Males two or more years old were outnumbered by one year
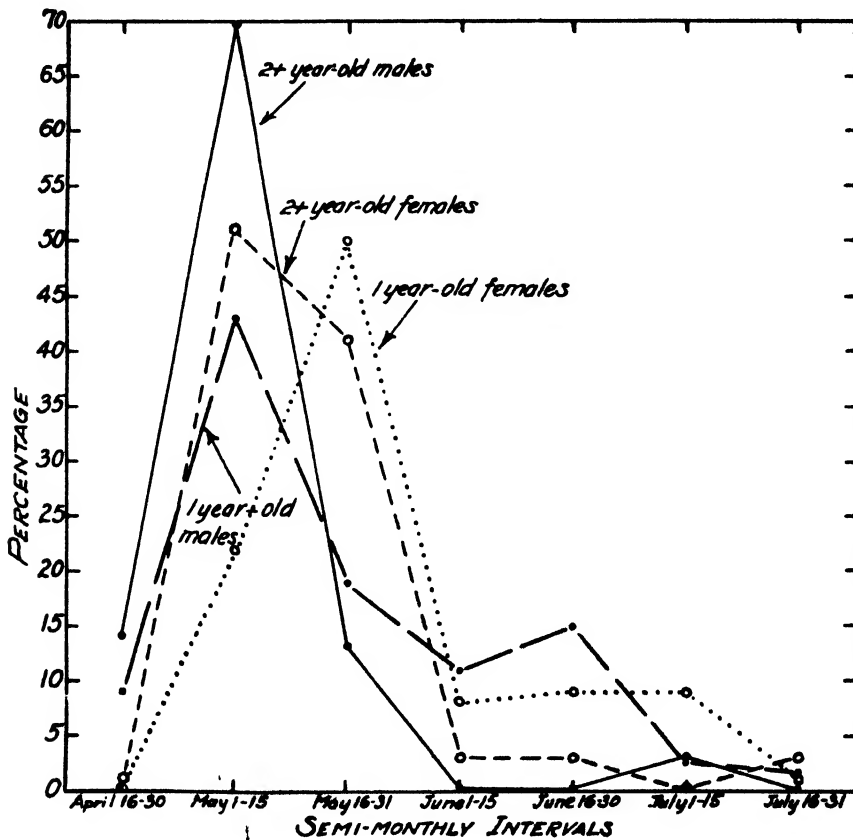
FIG. 5.—Graph showing percentage of all birds in each age and sex class arriving in spring migration on Hillcrest at semi-monthly intervals.

olds almost six to one, while the older females were outnumbered over four to one. Although the peak of arrival for males belonging to both age groups came during the first half of May, this peak was made up of 70 per cent of all the older males that returned to breed and only 43 per cent of the first-year males. The peak for the older females, constituting 51 per cent of all, came during the first half of May, while the peak for the one-year-olds, 50 per cent of all, came during the latter half of the month. Nearly all the new birds that arrived in time only for the second breeding period were young birds.

The above information shows definitely that while one-year-old birds of either sex may arrive along with the first birds of the season, older and more experienced birds constitute a great proportion of early arrivals, and younger birds predominate by far among the last to arrive and begin nesting activities. This order of arrival holds true also for the long-billed marsh wren, but in contrast the European wren is a permanent resident. The tendency to advance the time of beginning to breed with increasing age is shown further when arrival dates of individual birds in a series of years are compared. For 14 male house wrens that returned to breed for three to five years, the median dates of arrival in subsequent years are: May 13, May 9, May 4, May 4, and May 2. Similar information for six females that returned three or four years are: May 27, May 15, May 14, and May 11.

Return to Former Territories.—From Table 1, a strong tendency is evident for both adult males and females to return to their former territories, or at least to territories that overlapped in area territories occupied the preceding year. As example, note how the territories of male, A38398, in 1929 (89—Fig. 12) and 1930 (98—Fig. 14) overlapped part of his territory in 1928 (78—Fig. 11), and the territory of male, C68252,

TABLE 1.—RETURN OF ADULTS TO TERRITORIES USED THE PRECEDING YEAR

Comparisons Involving 30 Males and 24 Females	Males		Females	
	Number	Percentage	Number	Percentage
New territories overlapping former territories...................	30	· 58	17	52
New territories adjacent to former territories...................	6	12	1	3
New territories elsewhere on Hillcrest...................	10	20	9	27
New territories in Outfield........	5	10	6	18
Total...................	51	100	33	100

in 1931 (111—Fig. 15) and 1932 (122—Fig. 17) overlapped his territory in 1930 (101—Fig. 14). Further illustrations include male, C68910, whose territories in 1932 (119—Fig. 17) and 1933 (129—Fig. 19) overlapped his territory in 1931 (108—Fig. 15) ; also male, F58648, whose territories in 1933 (136—Fig. 19) and in 1934 (142—Fig. 21) overlapped his territory in 1932 (116—Fig. 17).

Often if the territories do not overlap they are adjacent to the area formerly occupied. Especially interesting is the sequence of territories of male, F45987, who nested six consecutive years on Hillcrest, alternating in such a way that three times his territories overlapped those of the preceding year, while two times they were adjacent, but not overlapping. The numbers of his territories in consecutive years are as follows: 1932 (118—Fig. 17), 1933 (134—Fig. 19), 1934 (144—Fig. 21), 1935 (157—Fig. 23), 1936 (169—Fig. 25), 1937 (177—Fig. 27).

In cases where males set up territories on Hillcrest having no evident relation to those of the preceding year, one might suppose that they went elsewhere because their previous year's territory was already occupied. In only two doubtful instances could this have been true. Information on the first arrival and beginning of activity in individual males of known identity is not always well established, but circumstantial evidence indicated that in eight and possibly all ten cases their former territories could have been taken over. No reason can be given for the males nesting in the Outfield rather than on Hillcrest, aside from a lack of a precise homing behavior. There are no records of adult birds being recovered in other localities away from this vicinity. In general, then, the odds are nearly three to one for male birds to return and set up territories on the same spot or immediately adjacent to where their territories were located the year before, and for those that do not do so to establish territories in other areas not far removed. The European wren likewise retains the same territory from one year to another and insures its retention by defending it against intruders at all seasons of the year.

The percentages of return for female house wrens do not differ greatly from the males, but there appears a slightly greater tendency for the females to wander (Table 1). The tendency to return to former nesting areas is further shown, however, in that out of 49 instances when comparisons are possible the females 33 per cent of the time selected for nest-rites some time during the breeding season the same box that they used at least once the year before.

In the Outfield, numerous records are available on birds that returned to nest in succeeding years. Although their territories were not mapped, the amount of shift from one year to another was readily determined from the distances between boxes that the birds occupied. There are 278 records for old return males and 279 for old return females. There are

likewise 182 records, males and females inclusive, showing the distance that young birds first nest from their place of birth; these birds were all banded as nestlings, so that their exact age is known. In a surprising number of instances, actually 22 per cent of all the records, these return nestlings skipped at least one year, and in four instances two years, before they were recorded as nesting. This could hardly be due to inefficiency in trapping operations as, in the case of adult birds, skipping a year occurred in only 7 per cent of all the records. Those birds that skipped one or two years before beginning to nest did not wander farther from their birthplace than did the others. Actually, of the four nestling birds in the Outfield that returned to nest in the box where they were born, one skipped a year before doing so. Skipping a year is therefore disregarded, as all records are compiled together in Table 2.

Approximately three-fourths of all the adult birds return to nest within 1000 feet (305 meters) of where they nested the previous season. A high percentage return to the same box where they previously nested. A higher percentage of males than of females return to the same place or the immediate vicinity. With males, only one per cent wander to a distance greater than a mile (5280 feet, or 1.6 kilometers), while six per cent of the females do so. The tendency for the female to shift around to a somewhat but not decidedly greater extent than the males has already been noted for the Hillcrest population.

The situation is quite different with nestling birds that return in later years. Of those where definite records are available, only 15 per cent

TABLE 2.—CHANGES IN LOCATION OF NESTS FROM ONE YEAR TO ANOTHER*

Distance between Nests in Feet (1,000 feet = 305 meters)	Return Males		Return Females		Return Nestlings	
	Number	Per-centage	Number	Per-centage	Number	Per-centage
Same box both years .	85	31	72	26	4	2
Less than 1,000	146	53	123	44	23	13
1,000–2,000	17	6	30	11	34	19
2,000–3,000	9	3	17	6	21	12
3,000–4,000	10	4	8	3	24	13
4,000–5,000	1	+	6	2	12	7
5,000–6,000	6	2	4 .	1	19	10
6,000–7,000	4	1	6	2	3	2
7,000–8,000	0	0	8	3	7	4
8,000–9,000	0	0	1	+	4	2
9,000–10,000	0	0	1	+	1	+
10,000–11,000	0	0	0	0	2	1
Total	278	100	276*	99*	154*	85*

*In addition to the changes shown in the table, 31 wrens changed the location of their nests more than two miles. The record of these changes, in miles (1.6 kilometers), is as follows: no return males; 3 return females (1%)—2½, 5, 6 miles; and 28 return nestlings (15%)—2½, 3, 3, 4, 4½, 4½, 5, 5½, 6, 6, 6½, 6½, 7, 7, 7, 7, 7, 7, 7, 7½, 8, 8, 9, 9, 10, 20, 35, 50, 700 miles.

return to within 1000 feet (0.3 kilometer) of their birthplace. The distribution of returns for each additional 1000 feet in radius is fairly uniform up to a mile. Between one and two miles (1.6 and 3.2 kilometers) the distribution becomes greatly reduced, and beyond two miles, records of recovery are very spotty. The reason for this is that the distance goes beyond the study area of the Outfield. One recovery is of special interest, that of 34-3901, banded as a nestling, June 14, 1934, at a box in the Outfield and caught by a cat on August 10, 1935, at Lexington, Missouri, where supposedly it had been nesting. Its sex is not known. Thus, a bird that hatched as *Troglodytes aedon baldwini* (Oberholser, 1934), when it became adult, nested well inside the range of *Troglodytes aedon parkmani*. Riddle—to what subspecies does it belong?

A previous study (Kendeigh and Baldwin, 1937, p. 116) found that 92.5 per cent of all living adult birds can be accounted for by those known definitely to return to the general locality where previously they had nested, but this is true for only 11.5 per cent of former nestlings that are believed to be still alive. The other 88.5 per cent of the former nestlings drift away into unknown regions. In this group females outnumber males about five to three. In Table 2, it is permissible to think of the percentage of returns as approximately equivalent to the percentage of the total living population in the case of adult birds, but not for return nestlings. Approximately 10 per cent of the young birds probably still alive returned and nested within two miles of their place of birth; the other 90 per cent went elsewhere.

In 15 out of 18 records of birds banded as nestlings that have returned and nested for two or more seasons, the amount of shifting between breeding seasons has definitely decreased with increasing age. The record of B96357, a male in the Outfield, is an example:

    1929, June 22—Banded as a nestling.
    1930, July 7—4000 feet (1220 meters) away from place of birth.
    1931, June 11—1000 feet (305 meters) away from nest-site of previous year.
    1932, June 8—100 feet (30.5 meters) away from nest-site of previous year.

The tendency appears to exist for young birds to scatter out for their first breeding season anywhere from the box in which they were born to potentially the limits of the species' range, but with the return nestling population being thickest in the general locality of their birthplace, and the maximum possible dispersal rarely if ever actually realized. Furthermore, after once having nested they are thereafter faithful in their return to the same location year after year. There is no evidence that juvenile house wrens establish a temporary territory before they leave for the south to which they return the following spring, although in the European wren young males may sometimes select a territory their first autumn. Juvenile wrens of *Troglodytes aedon* leave the territory of their parents within a few days after they become fledged, remaining there-

after, until they are ready to journey southward, in shrubby fields, forest edges, or dense thickets, often in small loose groups.

Homing Tendency in Nesting Birds.—Fifty-three experiments, mostly with males, were performed over the course of several years to test the homing ability of nesting birds (Table 3). Individuals were captured at their nest-box and transported various distances away before being released. Up to about a half-mile distance (0.8 kilometer) most male birds returned to their nest, but beyond that the percentage of returns fluctuated, although it was sufficiently high, even up to two and one-half miles (4.0 kilometers), to indicate that a tendency to return is present. This is presupposing that if such a tendency exists the birds are able to find

TABLE 3.—HOMING BEHAVIOR OR RETURN TO THE SAME BOX OR VICINITY WITHIN A FEW DAYS AFTER REMOVAL

Distance Removed in Miles (1 mile = 1.6 kilometers)	Males		Females	
	Number Returning	Number Not Returning	Number Returning	Number Not Returning
Less than ½	9	2	1	1
½–1	8	9	0	2
1–1½	5	3	1	4
1½–2	4	0	1	0
2–2½	1	1	..	..
11	..	..	0	1
Total	27	15	3	8

their way back successfully. In three cases when males did not return to the place of capture they stayed and nested within one-quarter mile (0.4 kilometer) of where they were released. In two other instances they renested one and one-quarter and two miles respectively (2.0 and 3.2 kilometers) from their first place of capture, after traveling in one instance two miles and in the other one-half mile (3.2 and 0.8 kilometers) from their point of release. Some attempt was made to study homing at various stages of nesting life, but the results are only suggestive. In half the cases where the males were taken away before they had nests and mates fully established, they returned to or near their old territories. That homing behavior is better developed after nesting is well along is indicated by seven out of nine males returning to nests containing young.

As for the females (Table 3), the proportion of returns in these homing experiments is very much less. However, in eight out of the eleven experiments they had not begun egg-laying and were newly arrived at the box. Of these eight birds, five stayed and nested within one-third

of a mile (0.5 kilometer) of the point of release, two returned to the box where they were first captured, and one went elsewhere. One bird in the process of egg-laying did not return. The only bird with young at the time of capture returned to them. If a larger number of females could have been removed while they were with eggs or young, very possibly a larger proportion would have returned, as the incentive to do so would then have been greater. The males had this incentive better developed in having their territories already well established or their nests begun.

III. ESTABLISHMENT AND DEFENSE OF TERRITORIES

WITH the establishment of a territory a male becomes intolerant of other males of the same or of competing species. He becomes a despot over the area that he claims possession. This despotism and defense of territory is exhibited in definite ways that can be analyzed.

Song.—Territory is established and defended chiefly by song (103, 106, 124, 178, 199, 208). Only the male sings, as is true also with the European wren and the long-billed marsh wren. The "territory song" of the house wren is but little different from the "nesting song," and both songs announce to other birds that the territory is occupied. The character of the "territory song" is difficult to describe, not only because of its intrinsic nature, but also because of its great variability. A representation may be diagrammed as follows:

The song is characteristically composed of a series of rich, bubbling, rapidly repeated notes, given with three or four or more changes of pitch. Sometimes the different pitch levels are not so distinct as the diagram indicates, but are slurred together in an ascending or descending manner. Commonly the song lasts two to three seconds. The song often begins with churring, guttural or sharp staccato notes or squeaks differing from the main body of the song, and occasionally the song is preceded by notes made by clicking the mandibles together. Sometimes the song also ends with squeaks or gutteral notes. Outside the normal range of intensity and pitch, even the main part of the song may become shrill and squeaky. This is especially true when the male becomes highly excited by the presence of a new female inspecting his nest. This series of high-pitched,

shrill, squeaky notes, which may properly be called the "mating song," is almost invariably indicative of a female's presence, and very likely stimulates her towards coition. The variation from the territory song that we call the "nesting song" is given after mating is accomplished and persists throughout the progress of nesting activities and to a small extent even until the bird leaves for the south. Not infrequently the two songs are nearly indistinguishable, but usually the nesting song is not so loud, not so long, not so high-pitched, and is not repeated at so rapid a rate. Occasionally the pitch changes as many as four times, but more often there are only two or three major variations in pitch level, and not infrequently the variability may be still further reduced to a single shift in pitch or none at all. Often the song is given in a listless or subdued manner, but at other times it is uttered with more spirit, especially in the presence of the female. It is seldom shrill or squeaky. This song serves in part to coordinate and regulate male and female activities at the nest.

The male gives other songs and call-notes. When mildly disturbed or annoyed he may utter a long series of slow sharp staccato notes nearly on the same pitch level. When more seriously disturbed, he has a scold: *"zzz-zzz-zzz-zzz-zzz-zzz."* His scolding against intruders around the nest is often not so vigorous or so energetically given as is the scold of the female. Both male and female have other notes that serve for intercommunication throughout the nesting period. Especially important is a *"churrr,"* given most often by the female, to which the male often responds by song or change in behavior. Sometimes this note is shorter and repeated as *"chur-chur-chur"* or *"urrr-urrr-urrr."* Occasionally it is a *"cherr-ee"* or *"kerr-dee."* All these variations seem to serve the same general purpose of notifying the male of the female's presence. The female has a series of squeaky notes that she gives when excited, as when inspecting a new box for the first time in the male's presence. She also has a short low whine that she gives on occasion inside the box, as when the male comes near at the end of a period of attentiveness while she is incubating the eggs. The male European wren, in contrast, troubles himself little with the brood nest and has less contact with the female after the incubation begins.

Both male and female quiver their wings, when excited. This is most pronounced during the mating process, but is also practiced when the birds are disturbed or scolding. The male may also quiver his wings when defending or advertising his territory by song. Another index of the male's degree of excitement is the position of the tail. During ordinary singing it is kept lowered, but may be raised to various degrees when the singing becomes very intense or in scolding. The tail is held quite vertical or even to an acute angle with the back during the mating activities.

Perhaps these wing and tail movements serve in addition to song and call-notes to convey meanings from one individual bird to another. Similar use of wings and tail occurs in the long-billed marsh wren and European wren.

The territory song is usually given on some conspicuous post, wire, shrub, or tree, often within ten feet (3 meters) of the ground but sometimes up to fifty feet (15 meters) above the ground. The frequency of singing may be some measure of the vigor of the male and of his chance for success. On June 16, 1939, two males (208, 210—Fig. 31) on opposite sides of a large elm on the front lawn were competing for territory. One bird sang seven times a minute, the other eight to nine. The latter bird seemed the more vigorous of the two, and he later won out. Eleven to twelve songs per minute is near the maximum. On June 4, 1929 (Fig. 12), male, B97018, had to defend his territory (90) against male, B56491, invading from box 3A (88). In a tree near box 9 the "two males became perched opposite and facing each other about 18 inches (0.46 meter) apart. Each took his turn singing his territory song, beginning as soon as the other stopped, and giving it with all his might. They appeared to be trying to out-do each other, although apparently no female was around. After a couple of minutes of this, one chased the other away and remained apparently to claim this as his territory henceforth."

Birds in migration seem not to sing so vigorously or so continually as on their territory, but the closer they get to their final destination, the more they are apt to do so. It is probable that while enroute during migration, they may discover likely breeding places, sing, and then disappear. For instance, on April 21 and 22, 1932 (Fig. 3), a singing male came to the evergreens on the front lawn, then wandered over to the flower garden near box 51, passed up to the trees in front of the laboratory, and finally flew off in the direction of the laundry and disappeared. The next day, another bird was first noticed singing in the ice pond woods, later came up to the rose garden south of the main house, then went over to the north side of the house, but on the following day was back at the ice pond woods and soon disappeared.

The song of the first males to arrive in the spring is imperfect and incomplete. This is especially true if the weather is not too favorable and there is little stimulation from rivals. In 1926, male, 57759 (58), did not reach full vigor of song until eleven days after arrival, and A34236 (59) not for seven days. They would sing sporadically for a day or two, then become silent and not even be seen, only to appear again for another burst of activity. By the time the females were due their songs were being given more vigorously. This imperfection in early singing is not due to immaturity, for 57759 was at least four years old. It seems more a

characteristic of early recrudescence each year and may be effected by periods of unfavorable weather. In other years the songs of males have reached perfection much quicker, due probably to stimulation from a larger population of competing males and to the earlier arrival of females.

The presence of a female is a distinct incentive to song. The male will give his territory song over and over again, day after day, in a purely mechanical manner until a female comes into view. Not really until then does he show any emotional excitement. The song is given more energetically, the mating song is interspersed, and males from adjoining territories may tune in. Competition between two males in adjoining territories becomes most vigorous when an unattached female enters the area (44, 52, 59, 64, 103, 105). The ideal of song perfection for the female bird or the manner in which the song may be most stimulating to her is difficult to judge. Nevertheless it appears there is at this point an opportunity for the factor of sexual selection, advocated by Darwin and in recent times by Huxley, to become exerted, for the female must make some choice as to which territory first to enter. The male whose song is most stimulating to her ears would seem to have the advantage.

The apparent purposes fulfilled by the territory song are that of notification to other males that the territory is occupied, of advertisement of the male's presence to females, and of inducement to the female to enter a particular male's territory in preference to the territory of some other male.

Nest-sites.—Since house wrens nest in cavities, the number of suitable nest-sites may be definitely limited, and their establishment and protection is an important function of territory and necessary in the acquiring of mates. The acquiring of nest-sites often involved the destruction and ejection of eggs or young of other birds already nesting there. The destructive tendencies of the house wren are analyzed in detail in a later section (p. 28). These nest-sites help to outline the shape and size of the territory, and usually two or three such nest-sites are available. The term "nest-site" is here used in a broad sense to include also the nest begun by the male. In the 214 territories studied, the number of nest-sites claimed by males for their territories at some time during the season was as follows: 38 territories had 1 nest-site, 64 had 2 nest-sites, 60 had 3, 34 had 4, 13 had 5, 5 had 6, and 1 territory had 7. In those territories with unusually large numbers of nest-sites (59, 78, 115, 136, 158, 168), the nest-boxes were situated fairly close together, there was very little competition with other males, or the males simply were restless and aggressive. Although apartment houses intended for purple martins, *Progne subis,* were available in certain territories, they were seldom used. To have but one nest-site in a territory definitely showed subnormal activity. Often in such cases it was a young bird coming to breed during

the second period, so that he was compelled to force his way in and carve out a territory. Several territories have been indicated where a bird, again a first-year breeder, had a temporary splurge of activity at a single box for a period of several days to a few weeks and then disappeared. Then again where suitable nest-sites were isolated, the bird got along with a single one. There are no known instances on Hillcrest of a bird nesting in a box and having extra nests in natural cavities, although such surplus nest-sites could easily have been overlooked. These extra nests are not utilized by the male for night roosting, but any one of them may be used for a second brood later in the season or for two simultaneous nestings with different females.

The house wren is surpassed by the European wren in possessing a surplus of nests. Twenty-five males over three years built 155 nests in that species, or an average of 6.2 nests per male. In both the European and house wrens the male builds the basal part of the nests, principally of small sticks, while the female inserts the nest-lining. In the long-billed marsh wren the male builds several nests, but these are not usually used by the female for nesting as she makes one of her own with only incidental aid from the male. Welter (1935) gives five as the average number of male nests per bird, while the number may run as high as ten; these numbers are in addition to the nests built and used by the females. In the European wren the fledged young sometimes use these extra nests for night roosts, and in cold weather males and females may roost together in old cocknests.

Possession of nest-sites is indicated in the house wren by the insertion of nesting material, usually sticks. A very few sticks will do, in some cases only a single stick has appeared sufficient to lay claim to a box. The male is by no means equally active at all his nest-sites. His activity usually centers around a single box to which he first attracts female visitors. At this box his nest foundation is usually best formed and has the largest number of sticks present. His other nest-sites contain stick nests built to a varying degree of perfection. An active male holding possession of these extra "dummy" nests visits them at intervals, sometimes once a day, sometimes days apart. A main purpose of these extra nests is to give an incoming female a choice of various sites for nesting, thereby insuring her retention, where otherwise she would more likely seek the territory of some other male. Baskett (1896) appreciated some such function for these extra nests in the house wren many years ago, and apparently they serve the same purpose in the European wren, but not in the long-billed marsh wren. It very often happens during the course of the nesting season that the male house wren's activity becomes so centered at other parts of his territory that he loses contact with certain boxes where he had previously been active. In such instances,

too numerous to mention in particular, another male bird has come in and taken possession. Occasionally the male will make a contest for retention, but usually the new male simply assumes possession without a struggle.

The insertion of sticks into a nest-cavity seems to be a regular act in the behavior pattern of establishing a territory, second in importance only to singing. This nest-building activity begins simultaneously with initiation of singing on the male's first arrival in an area. Either activity at times takes pre-eminence. Sometimes the male is so active inserting sticks that his singing is interspersed only at intervals. Then again he may sing continuously and insistently all day long, visiting the box frequently, picking up sticks and straws, but then often dropping them without taking them to the box. Where the two processes are more evenly balanced, the male, when stimulated by a female's presence in the neighborhood, may carry two or three sticks into the box every minute, singing in the air each time he leaves. A single male may show all three degrees of activity at different times, showing the variability of his emotional behavior.

New nesting-sites may be included in the territory at any stage in the nesting cycle. If a male is not soon successful in obtaining a mate, he may shift his activities to other boxes. When the female is incubating, the male may wander to another box and add it to his territory, as his time is not otherwise fully occupied. Number 57759 in 1926 (58—Fig. 9) alternated between two types of behavior and song, giving his nesting song for a time at box 11 where his mate was incubating, then going over to box 6 and giving his territory song. The male usually takes an active part in feeding young, so during this phase of nesting his activity at other boxes may be limited. Not uncommonly, however, the male may early desert his task of feeding, leaving it mostly or entirely to the female, in order to get started that much sooner with a second brood at another box with another female (27, 41, 59, 114, 170, 171, 183, 202).

Chasing and Fighting.—Competition for territory through singing involves outbluffing the other bird. Competition may also involve actual combat, as through chasing (59) and fighting (77). Kluijver *ct al* (1940) state that the European wren defends his territory by song and posturing. Welter (1935) describes not only song and posturing but also chasing in the defense of territories by the long-billed marsh wren. Actual physical combat and destruction of nests, as will later be described, appears much more prevalent in the house wren than in either of these other two species. Chasing in the house wren is less strenuous than fighting, and in many cases may be sufficient. Chasing of one bird by another implies fighting if the other bird is caught. Thus chasing in itself is threatening to a greater degree than is singing or posturing. Posturing in a

threatening attitude may precede the chase, and sometimes is sufficient in itself. When assuming a threatening posture, the male intently watches every movement of the other, flattens himself out on a branch, erects his back feathers, lowers his tail almost vertically and fans it out, and partially spreads or droops his wings. When actually chasing, the two birds become oblivious of their surroundings. They circle round and round, sometimes flying to within three feet of the observer. On one such occasion they flew against the window pane of an open garage door. In intervals between chases sometimes, but not always, excited singing occurs. Usually in such chases the invader leaves the territory, and when the pursuer reaches the boundaries of his territory, he turns back. Sometimes the invader may endure this chasing or may chase in turn so that he is successful in wresting away ownership over the area in dispute. If one bird catches the other in such flights, pecking occurs and the competition may change into physical combat.

The following account taken directly from the recorded notes at the time (July 25, 1931, Outfield) describes what takes place. This pair of wrens had young birds twelve days old, and another male attempted to wrest away part of their territory even though it was late in the season. "Both males were singing quite rapidly as we approached the box. They were chasing each other in short rapid flights. Between flights one male would alight in a tree and sing a very elaborate territory song as rapidly as possible. It seemed to take the other male several minutes before he was able to sing his full territory song. The female was a very interested onlooker, and we believe she entered the chase, as three birds were seen circling when the female was not feeding the young. The nestlings scolded continuously. The songs of the two males were very different. After thirty minutes one male was driven from the territory. The victorious male then flew fifty feet (15 meters) north and then fifty feet south of the box singing his territory song. He then flew to a wire in front of the box where the female was. She entered the box, and the male scolded and next flew to the northern limit of his territory. Soon after the other male left, the nestlings quieted down, although the male did not enter the box for one and one-half hours."

The above represents a defense of a territory already well established. The following description of an actual physical combat is between two males for the possession of a territory and a female early in the season, May 10, 1931. "As we approached the box, two singing wrens were seen flying around the front lawn in circles, one apparently doing all the chasing. They flew around in circles about ten times, the flight becoming slower and slower as if they were tiring. One flew to the foundation of the porch, followed by the other. They clasped each other with their feet and fought. Kramer approached to within two feet of both birds

and tried to catch them but with no success. While this was going on, a third wren, probably a female, came to the box carrying nest material. The two males stayed at opposite ends of the porch, and every time one came near the other he was chased away."

The following description is of the encounter between the two males indicated in the description of territory 77 where a new male came in and dispossessed a male already partially established at box 59. "They were piling and tumbling around, much as two boys in a scrap. One was bouncing on the other, which was turned on its back. The female of box 59 was nearby, more or less hidden in the bushes, and seemingly unaware of what was going on. After a few seconds of this struggle, which, however, may have gone on much longer previously, the two separated, and one drove the other down the lawn. Neither male sang during the struggle, but they gave some shorter notes."

Fighting between wrens had been recorded by many other observers, but particularly by Miss Sherman (1925). She gives some graphic accounts of such combats but describes them as occurring between females. In our experience, a female is very often nearby and may sometimes be involved, but the fighting is entirely between males. She further states that these duels may end in the death of one of the combatants and occasionally this has been witnessed, but she does not give details of the evidence. In our experience, one bird usually becomes exhausted before the other and flees. If death occurs, as it infrequently does in the wren's conflict with other species (pp. 29-30), it is probably due to a chance blow on the back of the head.

Evolution of Territorial Defense.—If the various actions involved in competition between house wrens for territory are arranged in order of decreasing strenuousness, they would rank as follows: physical combat, chasing, threatening postures sometimes with scolding, competitive singing, establishing nest-sites combined with advertising song. This may well represent a natural order of events in a psychological series as well as in an evolutionary one. Observations in territory No. 209 (Fig. 31) bear this out. On June 13 another male invaded the vicinity of box 74, and the owner chased it into the rose garden. For a short interval preceding the chase, however, he assumed a serious threatening posture, which the invading male appeared to disregard. On June 14 he again invaded and was again chased out. Perhaps this happened more times than was observed. At any rate, on June 18, when the same male invaded to approximately the same spot as five days before, the male, who owned the territory, scolded him from a foot away and assumed a threatening posture as before. The invading male behaved as if he expected a chase. He hopped out to the edge of the bushes and with a final threatening posture from the owner he left, although there was no chase. It looked

like a conditioned reflex type of behavior, the postures and chase being at first associated to produce a response which after some repetition was produced by the posturing alone.

In an evolutionary way, territorial behavior may have progressed in a similar manner. Physical combat represents the most primitive manner of competition but is associated with the chase, although song is usually absent. After a time the chase alone is sufficient to drive an invader away as it is a prelude to fighting. The chase is usually interspersed with excited singing or threatening postures, and one can well imagine that later in evolution competitive singing in turn would be sufficient warning. Finally, song of the same character, although not given in an excited competitive manner, but more in a mechanical manner for self-advertisement may be ample notification of possession so that wandering males will avoid the territory. The behavior patterns of the males have become conditioned in a permanent manner, doubtlessly ingrained by process of evolution in the nervous makeup itself, so that at their present high state of development the simple territory song serves the same purpose for which in ages past more frequent physical combats were required. Certainly it is of distinct advantage to the welfare of the species not to waste energy in combats needlessly when the same purpose may be fulfilled by less strenuous behavior responses. That energy is needed for other duties such as are involved in reproduction and self-preservation.

Destructive Tendencies.—Conflict between house wrens for possession of territory and especially for nest-sites may involve the destruction of nests of other birds already begun. Strange unmated males are frequently about. If a breeding male deserts his territory or leaves it unguarded, these males may come in, court the female, and even attempt copulation (59). The female may object in some cases (126), but often does not. The advantage to the male in assiduous defense of his territory is in the prevention of such adultery (116) and breakup of nesting. Unguarded nests not infrequently have the eggs removed (53) or even the young killed and carried out of the box (136, 150) by new males or males from neighboring territories. It would seem that this is a natural consequence of the normal tendency of the male to add other boxes to his territory during the course of his nesting cycle, which becomes especially pronounced when unattached females are about. It is the regular act of the male, when his brood of young has flown, to clean out the nest of lining, debris, and other foreign material exclusive of the stick foundation which he himself had inserted. Eggs or young, if present in desired boxes, would be removed in the same way as any other excess material, as the goal is possession of a clean stick nest foundation to show to incoming unattached females.

Destruction of eggs (11, 15, 59, 61, 64, 77, 137, 156, 160, 175, 182, 201) and young (29, 134, 137, 150) may occur even when the nest is defended, as invading males try to wrest away ownership. It is seldom that one can obtain direct evidence of destruction (134), although circumstantial facts often warrant accusations, as when a new male is observed in the area or later building at the box where destruction has occurred. In some instances (29, 59, 61, 64, 201) one even wonders if the male might not have destroyed his own nest in the excitement of competition with a new male or for a new female, but there is no positive evidence of this (see also Wright, 1909). The extent of this destructive tendency within the species is not great, considering that, out of 331 matings, eggs were destroyed in only 13 instances and young in 5. This degree of destruction is only 6 per cent.

There is no reason to believe that the house wren must compete for a food supply with other species, although that may be one factor for competition within the species itself. The wren finds its food in crannies, crevices, corners, under bushes, in the grass, and elsewhere, often in places that other species do not frequent. However, nesting-cavities are often scarce, and, as the wren practices multiple nesting, they must often be fought for. Since other species may use similar cavities, competition for them may be keen and destructive. On this area the bluebird, *Sialia sialis,* and house sparrow, *Passer domesticus,* were most important in this regard.

Bluebirds are often successful in the defense of their nest-sites (64, 84, 92, 190), and in frequent instances a bluebird's nest in or near a wren's territory will not be molested by the wren until the bluebird brood has left (60, 90, 106, 147, 190, 193, 210). The conflict between these two species is sometimes very vicious, however. The wrens may terminate the bluebird's nesting in a box very early (59, 62, 89, 195) or may throw out eggs (86, 99, 103, 137, 192) or young. The destruction of bluebird young has not been recorded on Hillcrest, but the following observations were made, May 31, 1932, in the Outfield. In this case the young were between 11 and 14 days of age. "At 4:00 P.M. a *pair* of wrens were going in and out of the box trying to carry out a dead bluebird. When found, the bird's head was on the perch and the body in the nest below the opening. The nest was all torn to shreds. The other three young in the nest were also dead, with their necks torn badly and some viscera torn out. Neither adult bluebird was about. The next day a wren's nest was begun on top of the bluebird's nest and the dead young, and on June 6 the first egg was laid."

The bluebird-wren feud does not stop with destruction of eggs or young but may involve death of the adults. In two instances (59, 137) adult bluebirds have been found dead in their nests. One was a male,

one a female. One was badly bruised on the back of the head and neck. The other had the feathers on the rump matted with blood which were still wet when discovered. The injury did not appear severe on the surface, but autopsy showed an internal hemorrhage in the abdomen. Within an hour a new male wren was seen and heard singing its territory song near the box. In neither case was the deed actually observed, but the circumstantial evidence is indicative. One wonders how the attack took place. Was the injury inflicted during flight, on the ground, or was the bluebird cornered inside the box? In both cases the dead bird was found inside the box, and here it would seem that the smaller agile wren would be at an advantage. An observation of Beckwith (1913) of a fight between a house wren and a house sparrow has a bearing here. He noticed that the house wren was much more agile and quick than the sparrow. The wren would fly directly above the sparrow and then pounce on it and sink its sharp beak into the sparrow's head and back while in flight. The sparrow would sometimes fall more than 18 inches (0.46 meter) in the air after being struck by the wren. Possibly the bluebirds were first attacked in flight, and then the wren pursued them into the box for the final blows. In the nineteen years of observation, there have been 150 attempts of bluebirds at nesting. Ten of these were unsuccessful due to wrens, which gives a percentage of seven. We have no record of bluebirds actually destroying either eggs, young, or adult house wrens.

The house sparrow and house wren are more evenly matched. Twice, according to our records, wrens were able to stop sparrows from nesting in boxes before eggs were laid. Once they threw out eggs (210), and once they were probably responsible for the killing and ejection of young sparrows from a natural cavity. On the other hand, there are at least thirteen instances where wrens did not start nesting in boxes until sparrows were through or had their nests removed by us. Three times sparrows destroyed wren eggs, and possibly once they destroyed a brood of young. These four instances constitute only about one per cent of wren nesting attempts. On one or two occasions extra nest boxes of the wren have had their entrances so clogged with sticks and wires that no bird larger than a wren could possibly have entered. It seemed this was primarily a protection against sparrows. There is an observation recorded (Smith, 1911) of a house sparrow entering a house wren's box, pulling an adult bird out, and dropping it exhausted to the ground. Wrens and sparrows did not come into conflict as frequently as wrens and bluebirds. Sparrow nesting was well along before wrens were well started, and an additional factor was our own efforts in destroying sparrow nests and favoring wrens by making the entrances of many boxes too small for sparrows to use.

Although the sparrow is a larger bird than the wren, the wren is

frequently successful in defending his nest. One observation in the Out-field, June 4, 1926, is worth recording. The wrens had only the fifth egg of their set. "Two male house sparrows were perched within a foot or two of the box. Every minute or so they would raise the feathers of their back and lower their heads and open their wings slightly as if to make a dash for the box. The male wren, which was scolding excitedly, would then dive at the one which apparently was contemplating a sally toward the entrance of the box, and on two occasions he succeeded in dis-lodging him, possibly with his wings, but I think also with his bill." Barrows (1889) describes several observations of conflict between wrens and sparrows. He mentions 180 records of sparrows molesting wrens and 39 cases where wrens resisted the sparrow, but he does not list in-stances where wrens had interfered with the nesting of sparrows.

Any species that nests in holes in the same habitat as the house wren is not immune from the destruction of their nests. Once I observed a wren enter a nest of a black-capped chickadee, *Penthestes atricapillus,* in a natural cavity, carry out an egg in its bill and drop it about ten feet (3 meters) away, thereby breaking it. Usually, I believe, the wren punc-tures the eggs with its bill and carries them that way, or the eggs may be left in the nest. While carrying on these destructive activities the wren does not sing but slips around slyly and unobtrusively. In this case the adult chickadees were absent until after the eggs were destroyed. Later in the season a wren, probably this same one, succeeded in getting a female here and they raised a brood of young (72).

Among non-avian species using holes, the white-footed mouse, *Pero-myscus leucopus,* is most important in competition with the wren. When a mouse gets started with a nest in a box, the wren rarely dislodges it (36, 84, 92, 102, 158). The mouse is active chiefly at night, and during the day is buried in its nest inside the box, so the two have actually little chance for physical combat. Only twice has evidence been available that mice possibly destroyed a wren nesting already begun. In one case (36) during egg-laying, the first three eggs were found gone the day the fourth was laid. The female wren deserted, and when the nest was next examined three days later, a mouse was found to have appropriated it. In another case (158) a family of mice was found in a nest on the same day that the absence of the eggs was discovered. After nesting has started, the female bird is almost always in the box at night, and usually this is sufficient to keep the mice away. On one other occasion a dead mumified wren was found as part of a mouse's nest. It is rare that one knows certainly just what happens, but in this instance the bird may easily have become entangled in the nesting material and died. Prescott (1916), Pierce (1925), and Frost (1925) have described similar cases of wrens

dying after getting their feet caught in nesting materials. Hancock (1911) tells of other instances of finding house wrens made into the nests of white-footed mice and states one case where the mouse, about ready to give birth to young, actually killed the wren.

Squirrels, particularly the red squirrel, *Sciurus hudsonicus,* not infrequently enlarge the entrance hole of empty boxes and build nests therein. Chipmunks, *Tamias striatus,* are small enough to enter boxes with bluebird-size entrances and are sometimes found within. Neither species is a serious competitor with the house wren for nest-sites— the red squirrel because it is not sufficiently abundant and generally uses larger cavities higher in the trees, and the chipmunk because it is chiefly a terrestrial animal. In no certain instance can destruction of eggs or young wrens be ascribed to either of these two species, although there is one suspicious case (132).

Wasps, *Polistes fuscatus,* and less frequently bumblebees, *Bombus* sp., also use similar cavities for their nests. Both seem effective in keeping the wrens away (158, 172) but not frequently enough to be important. In no case are they known to have forced the birds to vacate but must get established first to be successful in competition.

Aside from strife for nest-sites, the house wren competes with some other species, as far as I can tell, chiefly from annoyance at their too close proximity. Our first record of purple finches, *Carpodacus purpureus,* nesting in the region was spoiled by having the eggs punctured, probably by a wren. Robins, *Turdus migratorious,* occasionally build their nests on top of the wren boxes early in the season before the wrens arrive from the south. This may prevent the wren from occupying the box until the robins are through (54). In two instances, the destruction of robin eggs in such a location I have thought due to wrens (27, 178). There is considerable difference between birds as to their tolerance. In 1933, wrens started to nest in a box about ten feet (3 meters) away from an active robin's nest (130). There was constant conflict, and in spite of the robin's apparently greater clumsiness and the protection the wren had in its box, it soon became apparent that the robins were getting the better of the competition. The female wren laid only three eggs, then deserted. In 1939, a robin nested in a rose arbor less than three feet away (1 meter) from a wren's nest (box 49, 208). There was never any sign of conflict. The robin brood flew successfully on July 4 and the wren brood left six days later. I also recall an observation made many years ago where a pair of robins and a pair of wrens both brought forth their young successfully, although the robin's nest was directly on top of the wren box. Metcalf (1919) reports a similar situation for a robin's nest, with nesting of both species successful. There is no basic conflict between these species.

On at least two occasions song sparrows, *Melospiza melodia,* nesting in bushes near a wren's nest and sometimes feeding directly below, have resented the wrens' presence and chased them whenever they left the box. Other birds may accidentally affect a wren's behavior. Once a catbird, *Dumetella carolinensis,* perched on top of a wren box, kept the adult wrens away from their newly-hatched young for several minutes. Another time a male redstart, *Setophaga ruticilla,* hovered in front of the entrance to the box peering inside, and in spite of loud protestations from the wrens did not leave, it seemed, until his curiosity was thoroughly satisfied.

Other species than those already mentioned with which the house wren has been reported in conflict are:

> Mourning dove—*Zenaidura macroura*
> Flicker—*Colaptes auratus*
> Crested flycatcher—*Myiarchus crinitus*
> Eastern phoebe—*Sayornis phoebe*
> Tree swallow—*Iridoprocne bicolor*
> Barn swallow—*Hirundo erythrogaster*
> Purple martin—*Progne subis*
> Carolina chickadee—*Penthestes carolinensis*
> Tufted titmouse—*Baeolophus bicolor*
> Bewick wren—*Thryomanes bewicki*
> Starling—*Sturnus vulgaris*
> Maryland yellow-throat—*Geothlypis trichas*
> Scarlet tanager—*Piranga erythromelas*
> Cardinal—*Richmondena cardinalis*
> Chipping sparrow—*Spizella passerina*

Doubtlessly the list could be extended. Of the twenty species mentioned as suffering from the attacks of house wrens, eleven species nest in holes, and the conflict may be for nest-sites. Reasons for conflict with the other nine species is less obvious, unless it be simply annoyance at their occurrence within the wren's territories. The house wren is not always the aggressor but is sometimes the victim in these inter-specific encounters.

Some individual wrens are more aggressive than others in the defense of territories. Male, H18586, is a marked example of an individual with a behavior pattern of destruction and killing (137). In 1933, in our interpretation of the evidence is correct, he killed one adult bluebird, threw out two sets of bluebird eggs and one set of wren eggs, and destroyed three broods of nestling wrens, the latter all on the same day. Although individual differences in degree do exist, the same tendencies are inherent in all, and under proper conditions may become expressed. Destruction by wrens of nestlings of other wrens, bluebirds, and house sparrows is especially prevalent under conditions of high population or perhaps overpopulation. In the six years when no destruction occurred or where it might have been of a bird's own nest in the heat of sexual excitement, the average population of males was 10, with a range from 9 to 11.

During thirteen years when destruction of other nestings did occur, the average population of male wrens was 13, and ranged from 11 to 16, except for a not-too-certain case (59) in 1926 when the population was only 4. This is further evidence that it is inherently a problem of territory establishment and a desire for nest-sites for carrying on reproduction.

As there are individual house wrens that are especially aggressive, so also are there individual birds that have a lower competitive spirit. Instances of this sort will be noted in this paper, but such extreme cases as the two following accounts we have never observed. Taylor (1905) tells of a three-room apartment house, where during one year house sparrows occupied one compartment and house wrens the other two. During the next year the house sparrows' place was taken by bluebirds. All lived in peace and raised their families.

Another account is given by Smith (1911) of where house wrens found a half-built house sparrows' nest in a box placed on a barn. The wrens built the foundation of their own nest on top of it, but the house sparrows put in the feather lining. There was no fighting. The wren laid the first egg but the next day the sparrow also laid one, until finally there were four wren's eggs and five sparrow's eggs all in the same nest, with the eggs of the sparrow arranged on the outside. The sparrow did the incubating. All the eggs of both species hatched at about the same time, but the young wrens very soon disappeared. The sparrows were not seen killing or removing the young wrens, so the manner of their disappearance is a mystery. Although this incident is an amazing one, I believe it within the realm of possibility. Differences in the behavior of individual birds are often apt to be great.

There has been considerable discussion in print (Bird-Lore, Wilson Bulletin, 1925-1927) concerning the destructive habits of the house wren on other species. This even went so far as to induce some (Sherman, 1925) to advocate removing all nest-boxes and other encouragement for wrens around human habitation when other species of birds are also desired. Although many of the accusations made against this species were based on circumstantial evidence, they were generally well within the realms of possibility. Even if all accusations could be verified, nevertheless there is very little evidence that the house wren affects the established population of any species over a period of years, unless it be with the Bewick wren. The northward dispersal of this species appears to be hindered by the house wren, which in turn is probably limited in its southward distribution by the Bewick wren (Butler, 1891; Jones, 1903; Christy, 1924; Sutton, 1930). After 25 years of having a high population of house wrens nesting each year on Hillcrest, there is no sign of diminution of other species. However, to lessen the competition between species for nest-sites, there should always be a surplus of boxes available.

The Female's Role.—Territorial relations in this species are strictly for the male to perform and function primarily for the obtaining of mates. Other advantages of the territorial system are the avoidance by the female of distracting attentions from other males and a ready source of food supply for both adults and young. I am not sure that I have ever seen a female take an active part in the defense of a territory.

The female will act, however, in the defense of the nest itself. She is often more quick and vigorous in her scolding at intruders near the nest than is the male. On at least one occasion (126) she was observed to drive off another male wren that came too close to the nest-box.

Possibly the presence of pieces of snake skin or other similar shining material may be protective, and as these pieces are usually conspicuously placed in the nest-lining or on top or between the eggs, they are probably inserted by the female rather than by the male, since only the female has ever been observed to insert the nest-lining material. Pieces of snake skin are regularly present in nests of the house wren. Accurate statistics are not available, but in 1939 they were found in at least 12 per cent of the nests. The most conspicuous use of a snake skin was in box 54A (212) during 1939 when a large nearly entire piece was inserted three days before the eggs hatched. One end was wound around the eggs and the other end stretched over the rim of the nest toward the entrance of the box. Its conspicuousness appeared too well done to be without some definite function. As numerous house sparrows were continually about and not infrequently perched at the entrance and looked in, the skin may have served a real defensive function, although there is no evidence that the bird deliberately intended it for this purpose.

The female appears to have very little knowledge of the limits of the territory established by her male mate, and she goes pretty much where she pleases. For instance in 1930, the female at box 53 was seen to go for food into apple trees north of the farmhouse outside of the territory of her mate (97—Fig. 14). When a female goes into the territory of another male, she may be chased out if the male there espies her (121). When she goes into unclaimed areas, she is safe from molestation (59, 208). After a female by repeated excursions into unclaimed areas forms a persistent habit of going there, the male often follows, and by giving his territory song adds this area to his possessions. The gradual extension of territory No. 203 in 1939 (Figs. 31, 32) was partly brought about in this way. I have no record of where an established female by repeated excursions into occupied territories of other males has induced her mate to usurp such areas for her benefit. If an unmated female seems interested in a box where previously the male had been present only occasionally, he may turn his major attention to it for a period of days, even if the female does not stay. A female may even induce the male to

add entirely new outside boxes or nest-sites to his domain, and Welter (1935) describes a similar instance in the long-billed marsh wren. Sometimes a female may inspect nest-sites (169) outside of any male's active territory and without any male around at the time.

The appearance of an unattached female seeking a mate and a nest-site is a potent stimulation for male activity (15, 44, 52, 59, 65, 72, 75, 103, 105, 108, 168, 209) and often causes intense song outbursts or combats between males of neighboring territories. There is one record for the Outfield where three different males were caught within a few minutes one after another in the same box where they had been competing for the attentions of a new female for a couple of days. Apparently this box had not been definitely incorporated into any one male's territory. My observations tend to support Tinbergen's (1936) contention that much of the rivalry between males is not just for territory, as has sometimes been maintained, but also for the attention and attraction of the female.

It seems that any tendency of the female to be confined to her own mate's territory is due to (1) the nest being centrally located so that she does not need to go far for food, (2) the female being chased out of neighboring territories, and (3) the male varying the boundaries of his territory to follow her movements.

IV. CHARACTERISTICS OF THE TERRITORY

A WREN's territory is by no means a uniform area static throughout the season. One can never be certain that the territories as first established and mapped in the spring will be maintained through the year. Frequent observations show that the boundaries of a territory are definitely recognized by the male, but these boundaries, nevertheless, are frequently in a state of flux and change. The concept of territorial relations in this species should be a dynamic one with individuals often in strife to adjust their space relations best to meet the prevailing demands. There is very little time during the season that the male can afford to relax his attention, although after the young hatch perhaps changes are less frequent than at other times. The way territories fluctuate in size is best shown in the maps for 1931, 1932, 1933, 1936, and 1939 (Figs. 15-20, 25, 26, 31, 32). The territories established by the European wren likewise vary in shape and extent with the progress of the season, as Kluijver *et al* (1940) show in a series of maps, and probably a similar condition is true for the long-billed marsh wren.

Variability in Territorial Boundaries.—The time of arrival of a bird in spring migration affects the size and stableness of the territory over which it claims possession. The first arrivals may often wander over a considerable area before settling down at any one box. Male, A34236, in

1926 (59—Fig. 9; see also 64, 78) at various times during May sang his territory song over the area from the greenhouse to the main garage and from there to the southeast corner and may have even crossed Mayfield road for an inspection tour of the adjoining estate. Finally he returned to the point near where he was first seen on May 6 and settled at box 49, the choice of his female. As new birds came into the area, he gave up parts of his vast estate only after vigorous defense. While this may be an extreme case, still the first males that arrive investigate and attempt to claim a larger area than they are later able to hold. The wanderings of male, A34236, were probably so great because that year the number of birds attempting to establish territories in the area was unusually small. In ordinary years with normal populations the first males' wandering around must be limited to a very few days, as very soon a new influx of migrants occurs, and then to insure possession, each male cannot occupy a larger area than it is possible for him to defend with vigor.

Males that arrive late in the season must usually squeeze in their territories by usurping parts of established territories of other males and by taking advantage of unoccupied areas. A typical case is that of male, 36-38466, at box 1 in 1939 (203—Figs. 31, 32). These late arriving males are almost always first-breeders (p. 39), and they begin their territories by including a small area around a single box. After this is fully established they then expand in various directions and add new nest-sites, the amount and extent of the expansion depending on the favorableness of the habitat and the competition they meet from neighboring males. They may progress in certain directions by making only small additions on successive days. Of 17 attempts recorded of late arriving males to usurp the whole or part of another male's active territory, 11 were successful and 6 were not. In the latter case the males disappeared. The fact that nearly twice as many attempts were successful as failed indicates that the boundaries of the territories are adjustable and subject to pressure from competitors. In year-by-year maps of territories, where territories overlap, the portions relinquished by the one male are shown by broken lines.

Changes in Territories between Breeding Periods.—The greatest factor causing change in territorial limits is remating for second broods. Most of the males that renested, or actually 89 per cent, retained their old territories for the second breeding period, changing them only to meet pressure from incoming males or to accommodate their new mates. When a female chooses another box in which to raise a second brood, the male often becomes inactive in parts of his territory which he formerly held. In such instances, which are very numerous, new males coming in estab-

lish territories without difficulty, or neighboring males expand their territories in that direction without meeting serious, if any, competition. The amount of singing necessary to establish a new addition to a territory depends on the amount of competition. When there is no contest involved, part of a day to a day and a half is sufficient, but when there is dispute, two or three or more days are required.

About 11 per cent of the males that nested on Hillcrest during both breeding periods established disconnected territories at various times (42, 66, 67, 70, 125, 133, 148, 158, 162, 166, 168, 169, 173, 183, 185, 186, 212). They may have been unsuccessful in one locality and then suddenly shifted to a different place and established an entirely new territory. In many of these cases the male while caring for young wandered off into other regions and found a new female there, and so established a territory around the box selected by the female, forsaking his old area entirely. In one instance, partly to be explained by such a happening (168, 169—Figs. 25, 26), two males actually exchanged territories, but not their mates, for second broods. In other cases, the male has found his former territory usurped by another male when he became free from caring for his young, and so was compelled to set up a new territory, usually nearby. In the long-billed marsh wren new territories for rearing second broods are usually established in more open areas, but this may be associated with changes in the marsh habitat such as do not occur in the forest-edge.

Not all house wrens remain on Hillcrest to nest during both breeding periods. At the end of the first breeding period 23 per cent of the 173 males that nested on Hillcrest disappeared, and 24 per cent of the 176 males present during the second breeding period were new males that had appeared. Very often males disappear while caring for their young out of the nest. This exchange of males between breeding periods obviously upsets the spatial balance between the various territories.

Females likewise shift considerably from one territory to another as rematings occur for second broods. Of 144 females with first nestings on Hillcrest, 41, or 28 per cent, disappeared at the end of the first breeding period. Of 141 females present on Hillcrest during the second breeding period, 38, or 27 per cent, were new for the season. The percentages of females exchanged between breeding periods are slightly greater than those for the male.

Of birds that left Hillcrest at the end of the first period, 59 per cent of the males and 68 per cent of the females were birds presumably in their first breeding season, the rest being return birds that are known to have nested before. As the percentage of first-breeders in the total population was 65 for the males and 78 for the females, there was a slight tendency for first-breeders not to leave as frequently as adult birds, but

the differential was small and of questionable significance. However, of the new birds appearing for the first time to nest during the second period, 95 per cent of the males and 92 per cent of the females were in their first breeding season. These percentages are high enough to be worthy of notice. It is known from trapping operations that 12 per cent of the birds that disappeared and 12 per cent of those that appeared as new for the second breeding period nested in surrounding nearby estates in the Outfield for the other period. Certainly the very high percentage of young birds making their first appearance on Hillcrest during the second period must include many nesting actually for the first time. It is possible that the slowness of young birds in starting to nest is due to this being their first attempt, and the various physiological and psychological processes involved have not reached complete efficiency.

Trapping of adult birds at the Outfield boxes during both breeding periods furnishes much information as to the extent that males and females shift around between first and second broods. Out of a total of 115 records for males, 47, or 41 per cent, renested in the same box a second time, and 56 others, or 49 per cent, did not move over 1000 feet (305 meters). This distance is about that of the greatest diameter of Hillcrest, although nearly twice its short diameter. This total of 103, or 90 percent, shows rather close restriction of movement. Another 10 birds were scattered to distances up to 4000 feet (1220 meters); one bird shifted a mile (1.6 kilometers) away, and another a mile and a quarter (2.0 kilometers). The females showed the same reluctance for moving very far. Out of 206 records for this sex, 94, or 46 per cent, renested in the same box, 83 others, or 40 per cent, stayed within 1000 feet (305 meters); thus 177, or 86 per cent, can be said to have stayed on the same territories or to have merely shifted over to adjacent ones. Nineteen birds moved up to 2000 feet (610 meters) away, 9 birds up to a mile (1.6 kilometers), and, as in the case of the males, one bird moved as far as one and a quarter miles (2.0 kilometers). The amount of shifting between periods in general is not related to the age of the birds. Individuals known to have nested in previous years shifted to distances beyond 1000 feet to about equal extent as did birds in their first breeding season.

Size of Territories.—Males come to know the general area surrounding their territories, even when they make no attempt to include all this area under their control. To obtain this knowledge they go on scouting expeditions (58, 60, 203). When they are beyond the boundaries of their territories they do not sing, but move furtively through the bushes as inconspicuously as they are able. On these trips they often find other nest-sites, and they investigate boxes and plant cover in a very thorough manner. Often they enter the territory of other males, and ordinarily, if

seen, are chased by the owner to the limits of his possession. The invaders do not offer resistance, but as soon as they return to their own areas they proclaim their authority there by song. Probably the expansion of territory in any direction is preceded by preliminary trips of reconnaisance.

With the territories mapped, their areas were easily determined through the use of a planimeter. The maximum area occupied during each breeding period or breeding season was determined, even though in some cases parts of territories originally staked out by the birds were later lost to competitors. During eleven years when the territories were mapped separately for each breeding period, the average total size was one acre (0.4 hectare), the same each period, although actually the greatest number of territories fall in the size class of one-half to three-quarters acre (0.2-0.3 hectare). Of 178 territories measured, the distribution of different-sized territories is as follows:

Number of Territories	Size of Territories Acres	Hectares
4	–0.25	–0.1
13	0.25–0.50	0.1–0.2
59	0.50–0.75	0.2–0.3
36	0.75–1.00	0.3–0.4
33	1.00–1.25	0.4–0.5
18	1.25–1.50	0.5–0.6
5	1.50–1.75	0.6–0.7
3	1.75–2.00	0.7–0.8
2	2.00–2.25	0.8–0.9
3	2.25–2.50	0.9–1.0
2	2.50–2.75	1.0–1.1

During the course of an entire season, the territory covers more area at one time or another than it does during any separate breeding period. During four years when territories were mapped only for the season as a whole, the average size was 1.4 acres (0.56 hectare). Harrisson and Buchan (1934) found the size of territories in the St. Kilda wren to measure 0.6 to 1.0 acre (0.24-0.40 hectare). Kluijver *et al* (1940) found that territories in the European wren vary in size between 0.75 and 3.0 acres (0.3-1.2 hectares) ; while Welter (1935) estimates their size in the long-billed marsh wren at about 0.3 acre (0.12 hectare) for monogamous males and double this for polygamous ones.

The largest territory of which we have record is No. 58 (Fig. 9) which was for the entire season of 1926, and in its broadest extent covered 3.6 acres (1.44 hectares). Some very small territories were also observed, such as No. 179 and 215 (Figs. 28, 31), each 0.18 acre (0.07 hectare), and No. 204 (Fig. 31) which was 0.08 acre (0.03 hectare). Territory 179 was that of a bachelor male during the second breeding period. Territory 215, if accurately mapped, was small during the first

breeding season, but when the female deserted her eggs on June 20, the male quickly expanded it. Territory 204 was of a bachelor male who did not get a mate until late in June. Although 'frequently watched, he was never seen to go beyond the four or five trees immediately around his box during the ten days previous to his obtaining a mate.

When the average size of the territories during each breeding period (Table 4) is plotted against the number of territories established during those periods (Fig. 6), it becomes apparent that with an increase in number of males setting up territories there is a proportional decrease in the average size of these territories. When the number of males present is of intermediate size, that is, eight or nine, the size of their territories in different periods varies greatly, 0.65 to 1.5 acres (0.26-0.60 hectare). However, a line may be drawn through this wide scattering of spots to show the general trend. With populations of males varying between six or seven and eleven, a straight line relation appears to hold. During 1926 (Fig. 9) there was a lower population than any shown in the figure, and with only three males establishing territories, their average size was 2.0 acres (0.8 hectare). This high average, however, is due to the one bird in territory 59 covering 3.6 acres (1.4 hectares); the other two territories, 58 and 60, covered 1.2 and 1.1 acres respectively (0.48 and 0.44 hectare). There is very probably a maximum limit to the size of a territory de-

TABLE 4.—NUMBER AND AVERAGE SIZE OF TERRITORIES EACH YEAR*
(1 acre = 0.4 hectare)

Year	First Breeding Period		Second Breeding Period		Season as a Whole	
	Number of Territories	Size in Acres	Number of Territories	Size in Acres	Number in Territories	Size in Acres
1925..........	8	1.0	7	1.6	..	...
1926..........	..	...	..	...	3	2.0
1927..........	..	...	..	...	8	1.4
1928..........	..	...	..	...	10	1.2
1929..........	11	0.9	10	1.0	..	...
1930..........	..	...	..	...	11	1.0
1931..........	8	1.5	8	1.2	..	...
1932..........	9	1.4	6	1.2	..	...
1933..........	13	0.9	8	0.9	..	...
1934..........	9	0.9	9	1.0	..	...
1935..........	8	1.2	9	1.0	..	...
1936..........	9	0.9	8	0.65	..	...
1937..........	10	0.7	11	0.6	..	...
1938..........	10	0.6	11	0.65	..	...
1939..........	12	0.6	10	0.8	..	...
Average.......	9.7	0.96	8.8	0.96	8.0	1.4

*Number of territories is total for study area even though parts of some territories extend outside. The average size is determined from only those territories whose entire boundaries are known.

termined by the distance practicable for the wren to leave the box for feeding and to exert dominance without undue expenditure of energy. This maximum limit is not very definite, but from the numerical distribution of different-sized territories given above, one and a half acres (0.6 hectare) would appear normal, as would a minimum size of about one-half acre (0.2 hectare). In five breeding periods out of twenty-two the average size of the territories got as low as 0.6 or 0.65 acre (0.24 or 0.26 hectare), but no lower. Perhaps this represents a size of territory below which only exceptional individuals can tolerate nesting conditions.

The size of a territory maintained by a species may exert an influence on the population density of that species in the habitat, but the reverse is also true. The size of the house wren's territory is compressible with increasing number of birds present, at least down to a minimum. When the territories are reduced on an average to that minimum, resistance to invasion by more individuals becomes exceptionally increased (p. 33) and the population tends to be thereby limited. Similar observations on the influence of territory on size of population have been made for certain water-birds by Huxley (1934). Moreau and Moreau (1938) found that size of territory was indefinitely compressible in one species of Euplectes
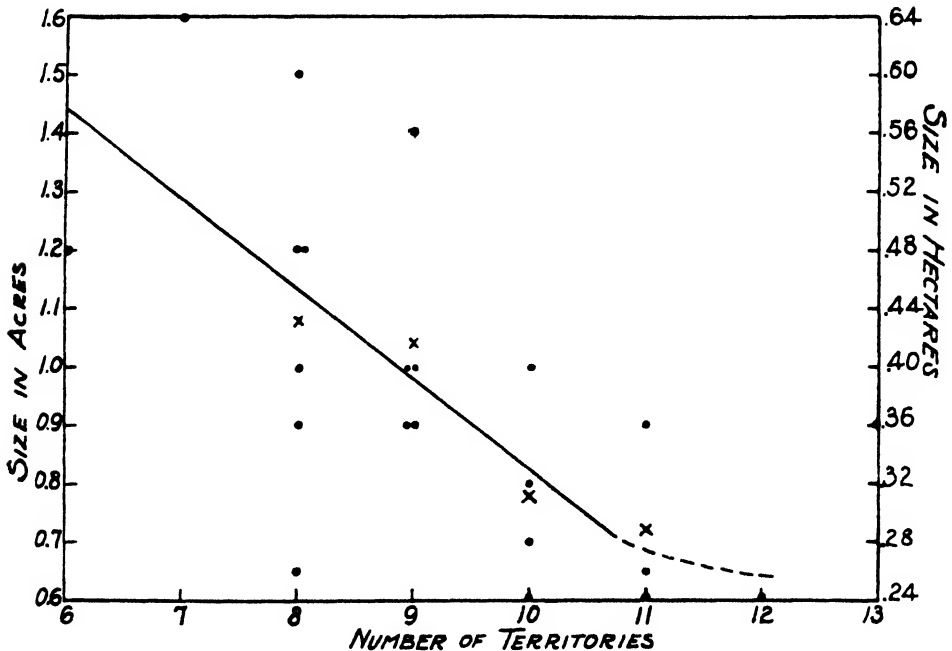
Fig. 6.—Graph showing relation between size and number of territories on Hillcrest. Each dot represents the average size for one breeding period, and each cross represents the average size for all breeding periods with the same number of territories.

but not in another, and therefore had different effects on regulating the size of the bird population.

On Hillcrest, 10 to 13 territories tend to reduce the territory size to near this incompressible limit and to represent a habitat saturated with this species. Even then many territories extended outside the limits of the fifteen acres. This does not mean that the entire area was included within the territories of different birds. Every year there were blank areas that remained unoccupied. These most commonly consisted of parts of the two apple orchards, the hard maple grove, the hard maple-beech woods, the vegetable gardens, and the front lawn. They represent less favorable habitats. The fact that the average size of the territories were not at the minimum (i.e. 1929, 1933, Figs. 12, 13, 19, 20) during some breeding periods with high populations is due to some territories when under pressure expanding into these less favorable habitats.

It is very difficult, however, to make any hard and fast rule, due to the individuality inherent in each bird. During some years with low populations and presumably reduced territorial pressure, some birds nested in those areas that we had labeled as less favorable. Likewise in some years with high populations, areas remained unoccupied that were normally filled. Actually the total area included in all the territories shows no consistent correlation with the number of active territories present but tends to remain constant. For example, in the second period of 1932, with only six territories, the total area included within territories was 7.2 acres (2.9 hectares), exactly the same as in the first period of 1939 when there were twice as many territories. Then again in the second period of 1925, seven territories covered 11.2 acres (4.5 hectares), while in the first period of 1933 thirteen territories covered nearly the same or only 11.7 acres (4.7 hectares). The point is clear that the size of the territory is flexible and, within limits, varies inversely with the size of the population present.

Observations show that a bird is not uniformly active every day in all parts of his territory. Parts of the territory may be forsaken for long periods of time and may or may not later be defended from the intrusion of another male. The wren is very much a creature of habit in much of its behavior. If food has been successfully procured in some one location, he is very apt to return again and again for hours or sometimes days at a time. This active portion of his territory, probably equivalent to the "sub-territories" or "food areas" described by Harrisson and Buchan (1934) for the St. Kilda wren, normally shifts gradually around from one side of the territory to another, so that the entire territory may be covered sooner or later. These active "food" areas are not always the same for both sexes, although some relation often exists between them.

V. REPRODUCTIVE VIGOR

THE URGE or drive for reproduction is a variable phenomenon. Normally the urge is non-existent during the autumn and winter months and reaches its height during late spring and summer. Some evidence has already been presented indicating that it develops more slowly in first-year breeders than in those that have nested before. Individual differences in reproductive vigor must play a part in the competition for territory and for mates.

Physiological Readiness.—Physiological readiness for breeding depends on the maturing of the gonads in both male and female. The time when this development begins each year has not been studied in this species, but if similar to other species, may begin in early spring while the bird is still in its winter quarters and may be nearly completed by the time the bird arrives in May. Aside from the maturation processes of the sex cells, there is the release of the hormones that exert a conditioning influence over the body as a whole and initiate the nervous processes that regulate the various steps in the reproductive cycle. It may well be true that these hormonal factors do not act in a complete manner until the birds arrive on the mating grounds. They may require for final effective action direct stimulation from the opposite sex. Perhaps this nervous and hormonal stimulation varies from day to day in a cycle manner, as Allen (1934) suggests, so that for consummation of the sexual act the cycles of two individuals must be in tune with each other. We have made no study of this subject. Often a female will accept a male and a nest-site after apparently a single inspection and begin carrying in nest-lining at once (25, 54). There is reason to believe, however, that a longer time usually is required to attain the requisite emotional or physiological pitch at which copulation occurs, both for a first mating early in the season (25, 41, 58, 102, 109) and for a later mating in July (90, 108, 176, 178). A female may persist in the neighborhood of a nest-site for several days and make several inspection trips or visits to the box, or she may visit different boxes before actually beginning her duties concerned with the initiation of reproduction and nesting. The female long-billed marsh wren appears similarly to require a period after arrival in the spring to work into the necessary readiness for copulation.

Non-Breeders.—Elsewhere (Kendeigh and Baldwin, 1937) we have analyzed the size and composition of the non-breeding (non-nesting) population of the house wren during the years 1920 to 1934, inclusive, and including both the Hillcrest and Outfield areas. For the first breeding period this was calculated to lie between 18 and 36 per cent and for the second period between 36 and 51 per cent of the total number of birds in the region. Over 80 per cent of the non-breeders were first-year

birds. Using the Hillcrest data only and for the years 1927 to 1937, inclusive, during which period the more efficient trapping in the Outfield would insure fewer wandering birds being missed, recalculation indicates that during the first breeding period, 15 per cent of the males and 13 per cent of the females did not make serious attempts at nesting. Similar calculations for the second period give 20 per cent of the males and 25 per cent of the females. These figures lie below the minimum given in the earlier calculations, but are for a smaller group of birds and on the Hillcrest area which may furnish special inducements for the birds to nest. The figures include 2 per cent each for males and females that omitted entire seasons for breeding, so that they were not trapped during the year at all. The figures for the males exclude from the non-breeding population those individuals that attempted nesting but were unsuccessful in obtaining mates. If these latter are included, the non-breeding male population rises to 28 per cent during the first period and 35 per cent during the second. Unpaired males were found in the European wren by Kluijver *et al* (1940) in territories lying next to mated birds, even birds that were polygynous. The presence of the non-breeding, but potentially breeding, population seems to have an effect on territorial behavior of nesting birds and to cause them to be continually alert in the defense of their possessions.

These non-breeding birds were not infrequently seen lurking around the nesting territories of other birds, but they did not often sing and were usually well hidden among the bushes and crannies which they frequented. Many, perhaps most, of them spent their time in shrubby fields, forest edges, bushy fence rows, etc., where nesting is usually not attempted. It happened not infrequently (4, 30, 38, 51, 69, 103, 179, 210) that some of these males got a temporary urge of procreation, established a small territory for a few days, then disappeared. In all such instances, the males were young birds. In some this urge lasted longer so that infrequently a male and female became active together at a box and attempted nesting activities (8, 25, 60, 154), although such attempts were frequently not carried through. This happened more often late in the first breeding period or during the second period. It is uncertain whether the birds were already partially paired at the time that they made their appearance, but they may have recognized each other as of opposite sex just previously and then sought a nest box. One or the other or both of them may have been potential non-breeders that through mutual stimulation acquired the initiative towards reproduction.

There is a record of six males who went through the entire season unmated (22, 28, 42, 52, 74, 165). Four of these birds had small territories, indicating probably that their reproductive vigor or energy was not high. All except one (165) were young birds in their first breeding

season. Four of their territories were in the upper apple orchard, and it is possible that females tended to avoid this area, although nesting there in other years was frequent. Altogether there are 75 records of "bachelor" males for single breeding periods. Of this number, 80 per cent were first-year birds. This percentage seems significantly higher than the percentage of first-year birds among the total males that did find mates (57 per cent). Female birds have often been observed to visit these males without staying to nest.

The point to be emphasized here is that there appear to be degrees of reproductive vigor manifested in different birds: (1) those who do not attempt to nest at all, (2) those in whom the urge occurs in sudden temporary and unsuccessful splurges, (3) those (males) who maintain territory throughout the season, but do not mate, (4) those who have mates and nests for a single period, (5) those that make two nesting attempts during the season, and finally (6) perhaps another and last group may be added consisting of those birds that become polygamous. Young birds predominate in the lower categories, most adults and many young fall in the upper ones.

Multiple Nesting.—Although the female ordinarily remains with the young until they become independent, there is a tendency towards the end of the first period when the nestlings are being cared for in the box for the female to begin preparations for a second brood. She may inspect other boxes either of the same male or of other males in different territories. If acceptable, mating may occur very soon, nest-lining inserted, or even egg-laying begun before she is through caring for her first brood. The number of instances when these early attempts at second nestings have been definitely recorded is not great (45, 46, 62, 68, 144, 146), and this kind of behavior has seldom been observed in the house wren. Only a few additional instances have been found in the literature (Holts, 1907). It is but a small step to actual desertion of the first brood by the female in order to start a second brood that much sooner, but desertion does not ordinarily occur without provocation. When the female leaves, the male will ordinarily care for the young alone. He mostly stops singing and applies himself assiduously to the task of hunting food for his offspring. However, he does not brood nor does he stay in the box at night. If the female deserts before the young have acquired self-regulation of their body temperature, death usually follows, but after a week's development, the male is often able to bring them off successfully.

In at least two cases, the female when disturbed has appeared to desert a nest, only to return later. In territory 46 in 1924, return female, 6882, came to box 51 on May 17 and had six eggs laid by May 25 when she was captured at the box. This disturbed her and she did not incu-

bate steadily again until May 30. The eggs hatched June 10, which was sixteen days after the last one was laid instead of thirteen days which is usual. If the five days of her absence be subtracted, it leaves eleven days as the incubating period. This is too short, and it seems probable that the female between May 25 and 30 must have been on the eggs part of the time, probably at night. Another case of interest was in territory 212 in 1939 where the young of a first-year female, 36-38455, hatched in box 43A, June 11-13. On June 17 she was caught and apparently deserted. However, the young birds survived, and the male fed them faithfully. The female must have brooded them at least at night. During the day she was occasionally seen and heard in the nearby bushes, and finally by June 26 she began gradually to regain her former behavior, and from then on she fed and cared for the young to an increasingly normal degree.

The tendency is better developed for the opposite situation to occur, for the male to become active at other boxes while he still has a first brood. Thus polygyny may occur. If the male participated more actively in incubation, polygyny would be far less likely. The percentage of matings that were polygynous in character was not large, being only 6 per cent. Likewise the percentage of unprovoked desertions not resulting in polygyny was negligible. The female almost invariably, although there are some exceptions, takes care of at least part of the young after they leave the box. As a rule the male aids the female in caring for the young in the box, but after the young leave, the male continues this aid only about half the time. When the male does not immediately do so, he begins at once soliciting a new mate, and the successful finding of one immediately may often explain the continuance of his inattentiveness toward the care of the young out of the nest. It sometimes happens that a male will divide his time between the care of the young off the nest and the seeking of a new mate, and may attempt to keep the young within or somewhere near to his territorial boundaries.

Polygyny is not developed to as great an extent in the house wren as in the European wren or long-billed marsh wren. Kluijver *et al* (1940) state that almost fifty per cent of the males in the former species become polygynous, a few even having as many as three mates at the same time, a condition we have never observed with the house wren. Welter (1935) found between one-fourth and one-third of the territories of the long-billed marsh wren to possess two females and a male. In this species, the females occupying the same territory were quite intolerant of each other even to the point of fighting. We have never observed this strife between females in the house wren, although they sometimes occupied boxes at the opposite ends of a male's territory (59). Welter also describes one case of multiple nesting by a female in the long-billed

marsh wren. Perhaps the greater development of polygyny in the European wren and in the long-billed marsh wren is correlated, as Kluijver *et al* suggest, with the male taking a smaller role in caring and feeding of the young, for in the house wren the male regularly shares in this duty.

VI. MATING BEHAVIOR

THE MECHANICS or manner in which mates are selected is of very great interest and is the chief goal in territory establishment. What determines whether or not two particular individuals will mate, and how is this accomplished?

The males are mostly confined throughout the mating season to relatively small areas and hence cannot seek out the females. Females are more free to wander and they initiate the mating procedure by coming into the territory of the male. They are attracted to these territories and appear able to recognize males of their own species from the nature of the song. The song varies in structural character between different individuals and at different times even in the same individual. We suspect these variations are relatively unimportant to the female as long as they can be recognized as of the species. Very likely the behavior of the sexes and the procedure they go through leading up to coition is mutually stimulating and functions in their emotional preparation.

Nest Inspection and Courtship.—The courtship behavior and inspection of territory and nest that is involved as the female arrives in the male's territory are similar for first and second broods. The following observations are quoted at length as they are quite representative. This is a case of *remating* for a second brood of the same two individuals at box 25 in territory No. 50, 1925 (Fig. 8).

June 21—First brood leaves box.

June 22, 23—No activity at box, both adults with young.

June 24—Male back giving territory song.

June 25—Male singing as yesterday but not so persistently.

June 26—Male removes lining from old nest, singing.

June 27-29—Male carries in many new sticks, singing.

June 30—Male persists in vicinity of box, often enters and carries out old pieces of feathers and straw from former nest-lining.

July 1—Male carried in sticks energetically for two hours this morning. A female appeared, inspected, left. So much carrying in of sticks seems unnecessary in an already well-built nest and may be simply a release of surplus energy and nervous excitement concerned in territory maintenance and getting a mate.

July 2—Male carried in sticks all morning. A female inspected once, left. Once when we inserted some feathers into the nest he "very indignantly" removed them.

July 3—Frenzied excitement of male as a female was here today to stay. Not certain whether the female is the same bird as during last three days. From 9-10 A.M. the male sang continuously, flying back and forth to all sides of the box and to the top, but not carrying in sticks. Was singing six times a minute, but when the female appeared his song increased in volume and was given

nine times a minute. Female uttered call-notes three times while at box 10-10:30 A.M. Male and female, flying from opposite directions, met in mid-air, then fluttered almost to the ground. Male gave a squeaky, coaxing, or mating song, the female acted shy and unconcerned, but seemed to notice what the male was doing. Female stayed 10-15 seconds at the box, inspecting it on all sides and within, and then when she left was pursued by the male. At 10:40 the male left for seven minutes probably for an inattentive period after food, and the female remained giving clucking notes. The male returned with a stick and met the female at the box. He flew off and dropped the stick without delivering it. At 10:55 both adults inspected another box in the territory. Both sexes fluttered their wings a good deal. Copulation probably occurred today, but was not seen.

July 4—Male back at box 25, singing all day. Female not very much in evidence, but occasionally in with nest-lining.

July 6—Male was here singing all day; female not very active.

July 7—First egg laid, probably four days after copulation.

When preparing a nest for a second brood, the male always removes the nest-lining inserted by his first mate. His new mate then carries in her own nest-lining. The female may come to the box voluntarily or she may be guided or enticed there by the male after she enters his territory. He flutters and flies toward the box ahead of her, goes to the top or to the perch, or may go in and out until the female begins her investigation. He then remains outside "squeaking" and very excited. If a female inspects a box, but then leaves and does not return in a few minutes, it shows she has some uncertainty. Insertion of nest-lining is a sure sign that the female is satisfied and is receptive of the male. The following observations at box 10 in territory No. 65 on June 27, 1927 (Fig. 10), give an idea of the relation between nest-lining and acceptance of mating. The male had been singing at this box for several days, although not very energetically. At 8:20 o'clock this particular morning a female approached and entered the box very deliberately before the male became excited or began his squeaking, mating song. This he gave on top of the box and on the entrance perch itself. The female during the next fifty-four minutes several times dropped to the ground, and returned to the box without nesting material. When the female was away the male would sometimes enter the box and would frequently fly after her when she left, as if to copulate. Finally on the seventh visit to the box she carried her first piece of nest-lining. Her next trip to the box was without lining material, but the following six trips were all with lining. Thus the transition in this case to continuous nest-building was a very gradual one, probably involving a change in emotional stage to a higher pitch. Until the female started regularly to carry in nest-lining the male persisted in giving his mating song, but after her routine became settled, he changed back to an excited and eager singing of his "territory" song, usually pursuing the female whenever she appeared. Copulation was not observed, but likely it took place this same day. The next day both birds were active at this box in the morning, but because of interference from

me transferred to box 9 at noon with hardly any interruption in activity. The first egg was laid July 1, four days after the female's first appearance.

Coition.—Copulation or coition does not occur until the female is ready and invites it. One such invitation may be described. The female crouched on a branch of a nearby maple tree and gave a series of squeaks varying between a monotone, an ascending, and a descending scale with shaking of tail and wings each time. This went on for a minute or two when the male responded with similar but softer notes, and approached her slowly. When within a few feet, the female would leave with the male in pursuit, or they would fly down to the ground. Probably copulation occurred then.

On another occasion at a different box, the squeaking sounds were produced artificially by kissing the back of the hand. An unmated female was near, scolding. She had recently inspected a male's box. The male on hearing these squeaks came over very excited, squeaking in turn, singing softly, tail upturned, wings a-flutter, and tried to copulate with the female, unaware that these inviting sounds were not coming from her. In the long-billed marsh wren it is usually the male that induces the female into copulation, but Welter (1925) mentions that occasionally the invitation comes from the female. Song attracts the female into the territory, but thereafter display is of greater stimulating value for the female. In the European wren the quivering wing display is also of importance for mutual stimulation leading to copulation, and the female has a short call that expresses her willingness.

The actual act of copulation has seldom been observed in the house wren. Probably it takes place on the ground or in low bushes, although sometimes in trees. There is no reason to believe that it occurs inside the nest box. Copulation probably does not occur immediately on the female's acceptance of the box, but apparently does so sometime that first day after the nest-lining has been begun. Possibly the act of preparing a nest-cavity for the eggs is stimulating in itself and is necessary as well as the excitement of the male to put the female in the proper condition. The male seems always most excited this first day, and sometimes this excitement continues into the second day but thereafter gradually subsides. Copulation may, however, occur repeatedly through at least the early part of the egg-laying period.

The following description of the copulatory act was made on June 4, 1926, at about 10:00 A.M. in the Outfield, the morning the fifth egg of a seven-egg set was laid: "The male wren flew to a branch of the tree in front of the box and gave his territory song in an excited manner. The female came out of the box and perched about two feet (0.6 meter) below the male on the same branch. She fluttered her wings like a young bird and made little cheeping notes and squeaks, keeping her bill open

all the time. The male quickly ran down the branch and copulation was consummated. It lasted only a few seconds. The male fluttered his wings rapidly and apparently did not rest on the female but held his body erect in a vertical position with his tail down. He then ran rapidly up the branch about three feet (0.9 meter). The female still fluttered her wings and cheeped and the male faced her, putting his bill almost on the branch in a crouching position. The female approached and the male fled. After a short chase in which the male succeeded in eluding the female, she flew to the field and I could not see whether she was feeding or gathering additional nest-lining. They then both flew to a small bush where the male chased a song sparrow. The whole scene lasted eight to ten minutes."

Female Discriminations.—The female exercises most of the apparent discrimination in the pairing of the sexes. Her first selection is of the territory to investigate which is advertised by the singing male. Perhaps the character of the male's singing and its stimulating force is here important. The next point where discrimination enters is in the selection of the nest-site. The extent to which the male has built the nest foundation of sticks seems not in itself to be of primary importance. Females have chosen nests in all stages of completion, although most frequently of medium size. Kluijver *et al* (1940) state that in the European wren the character of the nests begun by the male does have an importance. In the house wren the shape and size of the nest-site do not appear to be very influential, but this was not well tested, as practically all boxes erected were of similar dimensions. Of course, the cavity needs to have a certain minimum size, and cavities of too great size are also avoided. The location of the nest-site may have importance, and the females will examine this most thoroughly on their inspection trips. Perhaps the combination of these three characteristics gives importance to the nest-site. Certain nest-sites are favored over others, as mentioned elsewhere, and doubtlessly males in possession of these locations have an advantage in getting mates. Sometimes a female will examine two or three boxes in the territory of one male and not satisfied go to the territory of another male before finding what she wants (52, 90, 102, 108, 129). Thirdly, there is the eagerness and stimulation of the male and his physiological readiness for her. Miss Sherman (1925) considered the nest-site rather than the male of paramount importance in making a choice, but there is not much that can be discussed on this point as the physiology of mating needs detailed study and analysis. There is no plumage display except for wing quivering that is indulged in by both sexes. Perhaps all these factors are involved, but it is difficult to judge their relative importance.

Sex Recognition.—Sex recognition with the house wren seems to depend on a difference in behavior. There is no automatic recognition of

the opposite sex either through some unknown sense or by color, size, or form (Noble and Vogt, 1935). Only the male sings, so the female's recognition of him on his territory is not difficult. Call notes are similar in both sexes, although "churring" notes and rarely a little whine seem more often uttered by the female. The churring notes may have some sex recognition value for the male but not for mating purposes, as these notes are more commonly uttered after nesting has begun. No recognizable differences in plumage exist.

Non-singing males and sexually inert females have similar manners, postures, and behavior, and the adult birds cannot separate themselves sexually. A female seeking food in another male's territory is driven out as if she were a male on a scouting expedition. An observation is even on record of a male unexpectedly meeting his mate while foraging for food and chasing her to the edge of his territory until she, by non-resistance, permitted his excitement to subside. Once two birds, believed to be females, arrived simultaneously for an inspection of a box of an unmated male. The females seemed to vie for the male's attention. They ran along the ground and in the low shrubbery with wings spread and quivering. The male followed singing but not very far. He appeared bewildered and confused and did not respond sexually because of the exceptional situation. When a female comes to inspect a box for possible mating, the male sometimes does not get excited until her inspection has begun. He seems then to first recognize her as a female and may show her several boxes. Males on neighboring estates quickly respond to a bird as a female if she is so recognized by one male. The female's immediate starting to insert nest-lining after accepting a nest-site may have a value of further demonstrating her sex to her desired mate. After nesting has begun, differences in the duties and mannerisms of the two sexes probably allow individual recognition, as they become adjusted and accustomed to each other.

Further evidence that recognition of sex is primarily by behavior is available from an unusual observation made in 1939 (209—Fig. 32). A male on a scouting trip is quiet and inspects boxes in much a similar manner as does a female. So far as known, a male does not ordinarily inspect boxes occupied by other males active there. In this case, the male bird, apparently a non-breeder, inspected box 74 on July 4, and the active unmated male there behaved towards him as if he were a female. Four days later, this peculiarly acting non-singing male appeared again and in the company of the sexually excited male from box 74 inspected boxes 70, 74, 68, 54. There was no chasing and no attempt at copulation, yet otherwise the behavior was that of male and female. This pseudo-female would have been identified without question by us as a true female had the bird not possessed a red celluloid band around its leg in addition to an aluminum band which indicated not only its sex but also that it was

a return bird from some previous year. Attempt at capturing it was not successful.

Remating for Second Breeding Period.—When the first brood leaves the box the male and female may each continue to care for a part of the young. If a second brood is attempted, remating must take place whether it be with the same female or with a different one. The same relation between sexes occurs in the European wren. Each nesting is a cycle in itself independent of other nestings, so that a changing of mates is to be expected (Nice, 1930). In 70 first nestings terminating successfully and followed by renesting for a second brood by both adults, remating of the same individuals occurred in 40 per cent of the cases, while in the other 60 per cent of the cases new mates were secured. The whole mating procedure is repeated for each nesting cycle.

Perhaps it is worthwhile to consider the factors involved and the chances for a pair of individuals to remate for a second brood. Although we know almost nothing about it, it seems logical that if physiological rhythms are involved a pair of individuals who have successfully mated once and become adjusted to each other will be more likely to be attuned for nesting again than will two strangers. There may also be recognition of each other as individuals by physical characters or by mannerisms, as Lorenz (1937) has demonstrated for other species.

If the male aids the female in the care of the young out of the box both are ready for remating at about the same time, but if he does not help her, he often finds a new mate before his former female is free to return to him. In 42 instances where the action of the male was known, the male aided in the care of the young exactly half of the time. When he aided, he did not acquire a new mate for 10 days after his first brood left the box, never earlier than 7 days, and once he had to wait 23 days. Burns (1937) mentions a rest period of 3 to 6 days between breeding periods when the wren does not sing. This doubtlessly refers to the time when the male is temporarily occupied with young birds newly out of the nest and when the intensive singing for second mates and territory is not yet started. When the male did not aid the female in the care of the young off the nest, he usually began intensive singing at once and had a new mate in 8 days, not infrequently within a day or two, although once he had to wait 18 days. The above figures do not take into account simultaneous nestings by either male or female, nor do they reckon with birds unable to find mates at all for a second brood. Further analysis showed that when the males aided in the care of the young out of the nest, they remated with the same female in 65 per cent of the cases, but where they did not aid, they remated with the same female only 33 per cent of the time. The same principle holds for the female. In other words, there is twice the likelihood of the same birds remating

for second broods if both share alike in the full care of the young. There is interest in that both male and female of the European wren accompany the fledged young, but the male frequently does not feed them. However, he often attracts the young at night to roost in one of his extra nests. This has never been observed in the house wren.

In 57 instances for the house wren the interval between the first brood leaving the box and the female's first beginning of the second nest is known. This interval varied from 3 days before the first brood flew to 17 days after the young flew. Forty, or 70 per cent of all the records, are for an interval of 7 to 13 days after the young leave the nest with the largest number, 9, falling at 11 days. A similar time interval occurs between broods in the European wren and about two weeks in the long-billed marsh wren. It is quite possible that for some of the shorter intervals the female had earlier deserted her first brood, and it is also possible that for a few of the longest intervals the first visits of the female to her second nest-site were missed. The young house wrens are normally cared for by their parents for about 13 days after leaving the nest. It is apparent that the female does not seriously start a second nesting attempt until her first brood becomes nearly independent, but that she will often continue some care of them for a few days after beginning nest-building or egg-laying. The male ordinarily becomes active for a second nesting sooner than the female and has frequently been observed to alternate attention to the young and to singing around his proposed nest-site. Sometimes the male and occasionally the female care for the young off the nest within the boundaries of the territory, but the usual procedure is to conduct the young some distance away—beyond the territorial limits.

To return to the analysis of the chances for a pair of birds to remate, other factors must be considered. If a territory is isolated from other territories and the birds do not wander far in caring for their young out of the nest, both are likely to return to the same place to renest and they naturally remate (5, 104). When territories are close together or where a new male comes in, replacing the former one who may be caring for young, new mates or shifting of mates commonly occur. There is at least one case where two females exchanged territories, although not mates, for a second brood (10). There are also cases (56, 169) where the attraction of the old territory meant more to the female than did her former mate at a nearby box. The extent to which the adults conduct their young is concerned, as either bird may find new localities and new mates that take precedence over the old. The female is also less likely to attract the attention of her former mate if he has already found a new mate, although she sometimes does and polygyny occurs (169).

Remating in Subsequent Seasons.—Remating of the same individuals in subsequent years is, as one might well suppose, less frequent than for

the second brood during the same season. In the records for Hillcrest, there are only 14 instances where the same male and female have mated together again in subsequent years. Altogether there are 105 records of subsequent matings of males, so remating of males with their mates of former years constitutes only 13 per cent of the possible cases. There are 65 records for females, and a similar computation gives 22 per cent.

The record of matings between 36-38856, male, and 36-38040, female, is of exceptional interest in showing the highest degree of fidelity to each other. These two birds returned for three years, 1937-1939, inclusive, and each year they mated for two broods, thus mating together six times. The first four times were all at box 47, the last two times at box 79 and 43A. Two of the broods were unsuccessful, but neither adult mated with other birds. Altogether they raised twenty-six young to leave the box, their fertility being especially high the last year with nine young in their first brood and six in their second.

Male. A38398, and female, B45348, were mated together each of three years, although but once each year, and each time at box 51. Although the male was banded as a nestling in 1926 and was last heard of in 1930, he was captured only once with another female early in the season and no brood resulted. Female, B45348, likewise was recorded only once with another male in the period from 1928 to 1930.

The following record of male, F45987, is unusually interesting because he kept the same mate for both broods each year but had a different female each year except one in his long life. The record of his mates until his death in 1937 is as follows:

	First Period		*Second Period*	
1932	Box 54A	F45992	Box 54A	F45992 (?)
1933	Box 54A	H18587	Box 54A	H18587
1934	Box 43A	L24955	Box 75	L24955
1935	Box 75	L24955	Box 43A	L24955
1936	Box 47	L73248	Box 37	L73248
			Box 34A	34–86014
1937	Box 34	36–38389	. . . .	. . . .

Once he was polygynous, three times his broods were unsuccessful, and altogether he helped raise thirty-three offspring.

To illustrate the other extreme of a male with a great diversification of females for mates, notice the record of the mates of male, 48785. Incidentally this male returned to nest in the territory in which he was raised the year before, although it wasn't until he was three years old that he returned to nest in the exact box in which he was raised.

	First Period		*Second Period*	
1921	Box 25	(nestling)	. . . . . .	. . . . .
1922	Box 23	26520	Box 26	22987
1923	Box 47	6884	Box 47	6885
1924	Box 25	58024	Box 23	A87

If remating with the same individual in subsequent years were entirely a matter of chance, it would not happen so frequently even as indicated here, when one remembers the wide choice of mates possible. The fact that birds often do remate in following years is of more interest and requires more explanation than the acquiring of new mates. One important and obvious reason for birds not to remate in subsequent years is the failure of one of the pair to return, probably due to death. Twenty-six instances since 1921 are known for Hillcrest where both male and female, mated together one year, have both returned the following year. In eleven, or 42 per cent, of these instances remating occurred. It is worthwhile to attempt an analysis of why remating did not occur in the other fifteen cases. Three times the male was already mated with another bird at the time his former mate put in her appearance. Theoretically polygyny could occur under such circumstances, but there happened to be no such record. Twice the male did not appear until after his female had found a mate. In one case the male's activity at the time of the female's arrival may have been modified because of his recent capture at the box. There is also one record where the female found a mate in the Outfield, so it is uncertain whether she actually revisited Hillcrest. If these seven cases, where there are extenuating circumstances involved, are subtracted from the twenty-six instances noted above, then the eleven times the pairs remated constitute 58 per cent of the times they had opportunity to do so. Of the eight records where remating did not occur, two males mated with other birds on the very same day their former females arrived. Here the new females may have had a priority of only a few hours or even minutes where otherwise remating might have occurred.

In all instances where male and female remated in a following year, both birds returned to territories that overlapped the areas they occupied the year before. In the eight instances where remating did not occur the male returned to an overlapping territory only three times, and likewise the female only three times. In no instance did both male and female of the same pair return to their former territory. From this it seems that lack of remating is often due to a scattering of the birds into other, although nearby, areas, while remating is greatly aided by both birds returning to the same old nesting grounds. The possibility exists that where a female did not remate with her former mate she may nevertheless have returned to her last year's territory or visited her former mate on a new territory without succeeding in making a union, although actually there are no such records available of the female having done so. There is no evidence that the birds migrate and winter together in pairs, although it is possible that both may winter in the same region and

migrate over the same route. The "group habit" in this species has not been demonstrated.

The question naturally arises as to whether the birds are able to recognize each other as individuals from one year to the next and if this influences mating. It seems probable that they would more readily respond to familiar mannerisms or to fall back into old routines of behavior, if these were presented, than to work out new ones. Two individuals who have mated and nested successfully together one year might well attract and stimulate each other to a more certain degree than would strangers. If there is any truth in this principle, the effect persists from one year to the next to as great an extent as from the first to the second breeding period in the same year, since the percentage of rematings among individuals that renest is practically the same in the two cases, being 42 per cent and 40 per cent respectively. This problem, however, must for the present remain in the field of conjecture.

In spite of the fact that adult birds regularly return in following years to renest in the same locality and young birds occasionally return to nest at or near the place where they were born, there is no record of inbreeding between father and daughter, between mother and son, between brother and sister, between step-fathers and step-daughters, or between first cousins. Probably the chief factor that prevents inbreeding is the tendency for first-year birds to wander into other regions for breeding purposes. Actually only five nestling birds raised on Hillcrest have returned to nest on Hillcrest in subsequent years in the twenty-six years that wrens have been banded here. Close inbreeding is not out of the realm of possibility, however, and might very rarely occur, as any one of these five birds could have mated with a member of its former family group. Inbreeding can definitely be ruled out as a factor of any significance in the mating relationships of this species.

VII. TERMINATION OF NESTING

SEVENTY-THREE RECORDS give the median date for second broods to fly as August 11, the earliest being July 22 and the latest September 1. Since the young birds after leaving the box must be attended another thirteen days, the median date when the adult birds are through with reproductive cares is about August 24. With the flying of the young from the nests, they soon leave the territories and there is no longer need for maintaining them. Actual defense of territory begins to lapse even before the young fly, as competition becomes greatly lessened. This is in contrast with the European wren which maintains its territory throughout the year, although even with them its defense is at a minimum in August.

Both adults continue ordinarily to take their proper shares in the care of the second brood both before and after it leaves the nest. The incidence for desertion of second broods is higher, however, than of first broods (19), probably because, with the advance of the season, physiological changes are occurring inimical to breeding but inducive to moulting. In nine instances, females have deserted eggs or young at the median date of August 3. Twelve times we have record of males deserting also by the median date of August 3. Our impression is that males desert more often than we have recorded the fact in our notes and in a greater ratio to the desertions of females. Males that lack broods and mates for this period leave sooner than the mated birds, the median date being July 23 in 33 cases, with extreme dates of July 13 and August 10. Responsibility for the care of the young therefore prolongs the period of reproductive activity of males by another month. It is probable that the disappearance of these unmated males is in part responsible for the easing off of the territorial strain before the young are ready to fly. Since the median date for the arrival of males in spring is May 11, and August 11 is the median date for the flying of second broods, territories are of use in this species for only three months during the year. When the birds give up their territories they spend their time in shrubby fields and fence rows, brush piles, forest-edges, and similar locations until they are ready to migrate south from late August to October.

Territories are ordinarily defended throughout the breeding season, as is true also with the European wren and the long-billed marsh wren. Some of the most vigorous combats and competitions in song have occurred late in the breeding period (p. 26). One may reason from this that the territory has importance as a reservoir of food. However, strife among males is generally most vigorous early in each breeding period when the territories are first becoming established, and much of this rivalry is undoubtedly for mates. Singing is less vigorous after nesting begins but is continued automatically until the young leave the nest and on occasion becomes intense, if a newcomer challenges possession or a new female appears. Since this species has two breeding periods, this maintenance of territory throughout the first period has a value in allowing males more often to retain the same territories for the second period with less expenditure of energy and more certainty of success than might attain if a complete relaxation of territories occurred during the first period. However, maintenance of territorial defense generally continues through the second period, even though there is no further nesting and some males become negligent late in the season. Aside from the food value, maintenance of the territorial and mating behavior throughout each period makes polygyny possible. "Territory," then, is of primary importance in the lives, the behavior, and the nesting success of these birds.

VIII. HISTORY OF INDIVIDUAL TERRITORIES

IN ORDER to make available to others the vast amount of information that accumulated at the Baldwin Bird Research Laboratory from 1914 to 1939, case histories of territories of individual males each year have been compiled, and for many years, maps showing the boundaries and growth of these territories have been prepared. Complete data of all mating of birds on Hillcrest are also given. When the bird is a return from previous years it is always so indicated the first time it is mentioned in the case history, so that where there is no notation to the contrary the bird should be considered a new one on the area. These case histories are referred to in the preceding general account as supporting evidence for the statements that are made. It is my hope that they will be useful to others in compiling other types of information than here considered. The record for the first seven years is fragmentary and preliminary to the serious study that was begun in 1921. If for nothing else it has a historical and personal interest in showing the growth and evolution of an idea and of a method of study in the mind of its originator, Dr. S. Prentiss Baldwin.

1914

Two broods of nestling birds banded.

1915

Dr. Baldwin wrote (1919): "During 1915 I had banded every House Wren, old or young, on the farm . . . ." Records of adult birds in his notes are as follows:

Box 9	June 19	27739
		27740
	August 15	27740
		27782
Box 49?	August 14	27739
Box ?	June 8	27712
Box ?	June 21	27731
		27732

There were apparently 7 adult birds on the place, but no distinction between males and females was made. Dr. Baldwin was not then aware as to how sex could be determined in the species. Likewise the system of box numbers had not been well worked out.

1916

Box 49?	June 23	38491
		27739
Box ?	June 17	38479.

Due to absence, not all the birds were trapped.

1917

Box ?	July 1	38946
		38947
Box ?	July 3	44001
		44015
Box 51	July 4	44008
		44009

It is uncertain whether these 6 birds constituted the entire wren population.

1918

Beginning this year the trapping and recording of adult wrens became more systematic and complete.

Box 51	June 19	44100
		44008 return
Box 25	June 19	44515
		44516
Box 40	June 23	44525
		44526
Box 47	July 14	45205 female
		45206 male
Box 59	July 14	45207 male?

1919

Box 19 (9?)	June 17	44008 return
		44100 return
Box 25	June 17	45302 male
		45303 female

"He (45302) sang and carried on nest building by himself until driven out by 45349 and 45335."

	June 26	45342 male, alone, singing
Box 26	June 17	45206 male, return
		45311 female
Box 3	June 19	45322 female
		45324 male
Box 40	June 24	44526 return, mate not caught
Box 63	June 24	45334 female
		45335 male
Box 53	July 4	45335 male

Male, 45335, was here two days after his first brood left box 63. Dr. Baldwin believed this bird a female, but later records proved it to be a male.

	July 4	45349 male, building nest same day
	July 20	45349 male
		45303 female
Box 30	August 2	45334 female, mate not caught

1920

Box 49	July 15	45955 female
		45335 male, return
Box 25	June 17	45303 female, return, two broods here
		45342 male, return, two broods here
	July 29	45303 female, return, second brood
Box 53	June 22	45968 male, alone, nest building
	July 5	With female, 45325, return
	July 16	46013 male, alone
	July 22	46030 female
Box 63	July 5	45988 female
		45335 male, return
Box 47	July 13	46006 female, incubating
	July 25	45349 male, return
Box 6	July 14	46010
		46011
Box 37	July 24	45955 female
		46032 male
Box 59	July 28	45968 male
		45325 female

1921

Territory No. 1.—Male, 45963, a return nestling, was at box 3 by May 19 and at box 6 by May 27. About May 22, a female, 21212, came to box 3 and their brood flew June 26. On June 17 at box 6 the male obtained return female, 45303, whose young had flown from box 25 only 5 days before, and they raised a second brood by July 22. He was thus polygynous in part. During July the male's place at box 3 was taken over by the male who came from box 25 (2).

Territory No. 2.—Return male, 45342, came to boxes 25 and 26 by May 4 and got return female, 45303, very soon. Their young flew June 12. While busy feeding his young out of the nest a new male (3) usurped his territory, so he moved over to box 3 on July 2, taking it away in turn from the male formerly here (1) who was busy with young at box 6. At box 3 female, 21206, whose young at box 63 had flown 9 days before, came on July 4, and their brood flew August 9.

Territory No. 3.—Male, 21315, came to boxes 25 and 23 on June 16 and usurped the territory of the male here earlier (2) who was helping to care for his young out of the nest. Female, 21213, whose young had flown 10 days before from box 59, came to him at box 25 on June 29, and they raised their brood to fly on August 5.

Territory No. 4.—Male, 21271, was active at box 30 from at least June 18 to July 3 but did not get a mate.

Territory No. 5.—Male, 21231, was at box 37 by May 17 and at box 40 by May 27, and a female, 21211, came to box 37 by May 22. Their first brood flew June 30. The male (same one?) was back on July 3, and the same female came back on July 6, only 6 days after her young had flown, and their second brood left the box on August 22.

Territory No. 6.—Return male, 45968, was probably at box 75 by May 11, but was not very active. Sparrows started to build here on May 27, but the male returned May 30-June 1 and removed most of their nest. He was at box 47 by May 16 and return female, 46006, came May 22, but on June 16 their young were destroyed and removed by sparrows. The male again shifted back to box 75 and his former female came to him here the next day. However, about July 17 or 18 she deserted her young, which were 9-10 days old, for some unknown cause and went to box 68 (9). The male at box 75 succeeded in bringing off the young alive on July 23. This male was polygynous, as it was probably he who had another brood at the same time at box 47. He was not captured at that box. After his first nesting at box 47 was destroyed on June 16, he threw out the nest-lining on the 18th, and had a female, 21294, here July 1. He deserted this box about July 18, the same day he was given full responsibility of the young at box 75. The female brought off the young at box 47 on August 7. Several days after his young at box 75 had flown, the male occasionally visited his brood at box 47.

Territory No. 7.—Male, 21232, was at boxes 49 and 51 by May 17 and had a female, 21207, at box 49 by May 23, and their young flew June 29. Perhaps he helped care for the young out of the box; anyway he was replaced on his territory by another male (8) and disappeared.

Territory No. 8.—Male, 21264, seems to have been active first on May 31 at box 57 where male, 48775 (9), had deserted on capture, May 25. His appearance here possibly coincided with that of a female, but they did not stay. The female was possibly the same bird, 21234, who came to box 53 to stay with him on June 2, again after another male, 45335 (10), had been caught there and deserted on May 29. On June 25, 4 of the 5 young at box 53 were destroyed and removed by an unknown agent, but the remaining young left on July 8. The male was around box 59 on June 27, but did not stay and retained some activity at box 53 through July, but on July 2 he was caught back at box 57 which he had visited off and on during June. On July 4 he went down to box 49, replacing the male (7) who had a first brood leaving there 5 days before. Here his former female returned on July 8, the same day her single young bird left box 53, and they started a second

brood which flew August 14. The single young bird that left box 53 may have died, as it was heavily infested with lice and below normal in weight.

Territory No. 9.—Male, 48775, was at box 59 by May 11 and had new female, 21213, here May 14, and their brood flew June 19. By May 25 he was also active at box 57, but was caught and soon replaced here by the male from box 53 (8). On June 11, a male, probably 21225, contested with him in song around box 59, but the next day this other male went to box 57 where he was caught and deserted. Here is a case of a male coming in to set up a territory, but, running into competition with two males (8 and 9) was unsuccessful. Although 48775 had probably been at box 68 between May 20 and 22 he did not return for much activity until June 18. He obtained on July 17 return female, 46006, who had just deserted her young at box 75 (6). They attempted a brood, but it was destroyed by a storm August 6. After the male's first brood flew from box 59, male, 21264 (8), was sometimes active at this box, although on July 11, 48775 was also here.

Territory No. 10.—Return male, 45335, was at box 63 by May 11 and had female, 21206, here about May 18. On May 28 and 29 he was active at box 53, but, when caught, he shifted back to box 63 where his young flew June 25. The male probably did not help to take care of the young out of the box, as on June 27, he showed a female, 21212, boxes 63 and 63A, and she chose box 63A where their young flew August 6. These two females changed places for second broods, as 21206 went to box 3 and 21212 had her first one fly from box 3 (1) only the day before she came to box 63A. However, 21212 did not lay her first egg here until July 5 and so probably attended to her young from box 3. Possibly also her polygynous mate at boxes 3 and 6 helped in their care.

1922

Territory No. 11.—Return male, 45335, was at box 3 by May 4 and had a female here about May 15, but by June 2 her eggs were destroyed and she was gone. The male was caught on June 8, and he also deserted inside of another day or two. On June 19 he was caught at box 25 and died in the holding cage.

Territory No. 12.—Male, 22995, was caught in the greenhouse April 24 and was at box 6 by May 27, but when caught there on June 8 he deserted. Probably on this date he transferred to box 25 and may have been there earlier. Possibly he was responsible for the destruction of eggs there between June 5 and 8. He had a female, 26520, visit here on June 16, but after being caught on June 19, he was not recorded again during the season.

Territory No. 13.—Since males at both box 3 (11) and box 6 (12) left soon after June 8, there was a free area here. Male, 26523, appeared at box 6 by June 16, but when caught on June 19 transferred to box 3 the next day. A female visited him there, June 29, but did not stay. He also disappeared.

Territory No. 14.—With the male gone from box 6 (13) on June 19, a new male, 26600, came in by June 24 and had female, 26595, here by July 2, and they raised a brood by August 9. After the male disappeared at box 3, 26600 had some activity there July 8 to 13, being frightened away by capture on this latter date. On July 27 the male from territory 20 whose first brood left box 47 on July 10 and whose place there was usurped by another male, appeared at box 3, was caught, and did not stay.

Territory No. 15.—Male, 48785, a return nestling, appeared at box 25 by May 4 and at boxes 23 and 26 by May 20. About this time a female, probably 26520, appeared and very likely her presence inspired the male's activity at boxes 23 and 26, but she stayed at box 25. On June 5 one of her eggs was gone, and on the 8th all the eggs had small holes pecked in them, possibly by male, 22995, who transferred to this box on June 8 from box 6 (12) after he had been caught and banded at that box. Male, 48785, went immediately to box 23 where he was caught also on the 8th. He transferred to box 26 by the 13th and was caught there on the 19th. Meanwhile at box 25, 26520, probably the same female who was here

before, came to the male, 22995, on June 16, but on the 19th both deserted after being caught at 11 A.M. There appears to have been a lively competition involved for both box and female on this date as return male, 45335, came over from box 3 (11) and was caught here at 2 P.M., accidentally dying in the holding cage. It was also on this date that 48785, probably excited and involved in this competition, was caught at box 26 nearby. Three days after female, 26520, deserted box 25, she had remated with 48785 and had laid her first egg in box 23. Their brood flew July 25. The male probably did not aid much in their later care, as on July 17 he was again active at box 26, and a female, 22987, who had deserted both box 53 and box 47 on July 13 and box 49 on the 15th (21, 24) when caught during inspection trips, came to him there on the 18th. However, her eggs were removed and destroyed by some unknown agent July 29 and nesting was over.

Territory No. 16.—At box 25 a male, 26638, and a return female, 45303, appeared on June 29, the female coming 12 days after her first brood at box 30 (17) had flown, and they raised a brood by August 4.

Territory No. 17.—Return male, 21231, arrived at box 30 by May 4 and had return female, 45303, about May 8, quite early. Their young flew June 17. He apparently disappeared while caring for them, thus avoiding the strife at boxes 23, 25, and 26 around June 19 (15).

Territory No. 18.—Male, 26504, was at box 9 by June 10, had female, 26542, by June 13, and their young flew July 19. The male stayed more or less around for another 10 days, but there were no further developments.

Territory No. 19.—Male, 26512, was at box 37 by May 4, had return female, 21212, about May 13, and their young flew June 21. On June 24 and again on the 29th there were two birds at the box but neither was identified, and on July 2 female, 21212, was back, 11 days after her young had flown, and laid her first egg. The male, probably 26512, deserted July 22, but the young flew August 4.

Territory No. 20—Male, 26546, was at box 47 May 4, and female, 22988, was here with her first egg on June 3. On the 5th, two marked eggs out of three had disappeared, but the female stayed to lay seven more (ten in all) and her young flew July 10. The male, while probably caring for young out of box, was displaced by a new male usurping box 47 (21). This male showed up at box 3 in late July, but did not renest.

Territory No 21.—At box 47 there appeared on July 13 a male, 26601, and a female, 22987, the latter having deserted box 53 (24) at 7 A.M. that morning when she was caught nest-building. She did not stay. A female, 22989, whose first brood had flown from box 52 on June 30 and who was caught at box 63A with a nest ready for eggs on July 13 (23), had her first egg in box 47 on July 17 before any lining had been inserted, and the pair probably raised the brood successfully. Which male fertilized her eggs, 26601 in this territory or 45342 in territory No. 23?

Territory No. 22.—A male, probably 26629, was at box 75 from early June to late July without getting a mate.

Territory No. 23.—Return male, 45342, was at box 63 by May 4, but had no further activity here all summer. He was at box 52 by May 20 and at box 63A by May 27. At the latter box he had some activity intermittently all during June. At box 52 he had a female, 22989, about May 23, and their brood flew June 30. Possibly both adults cared for the young out of the box, but both were back at box 63A on July 9. However, with her nest-lining well along, the female was caught on July 13 and deserted, later appearing at box 47 (21) on July 17 and laying her first egg there on that date. The male also left about the same time.

Territory No. 24.—Return male, 21264, was at boxes 49, 51, and 53 by May 4. About May 16 a female, 22987, came to box 53, and their brood flew June 24. The male was intermittently active at boxes 51 and 49 all season. The male probably did not aid in the care of the young out of box. On July 6 he had a female near box 53, and again on the 8th, 9th, 12th, and on the 13th. She was caught and proved to be his old mate, 22987, who the day before had started a nest-lining.

However, she deserted and appeared next at box 47 (21) at noon the same day. She deserted box 47 also and returned to box 49 with 21264, but when again caught she again deserted and showed up at box 26 (15) on July 18. On July 17, the male had another female at box 53, but she did not stay. From July 20 to 24 there was a female around, and on the 27th, female, 22988, whose first brood had flown from box 47 (21) on July 10, laid her first egg. Although she had laid 10 eggs in all at box 47, she laid only 3 here. Her brood probably left successfully.

Territory No. 25.—Return male, 48775, appeared at boxes 59 and 57 by May 20 and had a female, 26502, accept box 59 the same day. Their first brood left June 26. While caring for his young the male was forcibly displaced from his territory by an incoming male (26) and disappeared from the area.

Territory No. 26.—On June 29, a male, 26553, and possibly also a female appeared at box 57, and there was competition for its possession with the male from box 59 (25). Male, 26553, won out. The identity of the female on June 29 is uncertain, but female, 26502, came to box 57 on July 5, nine days after her first brood had flown at box 59 (25), and they raised their brood by August 7.

1923

Territory No. 27.—Male, 6899, was at box 3 by May 14 and had a female, 6881, here by May 23. Did this male destroy the robin eggs on top of box 52 May 29-31? On June 17 both adults were captured at box and deserted their 3-4-day-old young. The male then spread his activity down to box 63A where up to June 1 sparrows had been nesting, and on the 30th he had a female, 57798, there. He ceased activity at box 3, and between June 24 and July 1 he persisted around box 53. On the latter date, although his new female at box 63A had just laid her second egg, he was interested in another female, 6885, recently unsuccessful in box 25 (29), who had come to inspect box 53. Both were caught and neither stayed thereafter, the female, 6885, going down to box 47 (35) on July 4 and the male returning to box 3 on July 2 and 3, and then back to box 63A where he helped to raise his brood by August 4.

Territory No. 28.—Male, 6893, was at box 6 by May 29 and at box 11 May 30. At box 11 the last of several sparrow nests was removed May 25. During June the bird vacillated between the two boxes, but between June 28 and July 8, he was displaced at box 11 by a new male (30), so he confined himself largely to box 6 until about July 23 when he was last recorded. There is no record of a female having visited him during the entire season.

Territory No. 29.—Return male, 22995, was caught in the greenhouse on April 24. He was active at box 25 by May 10 and a female, 6885, appeared here by May 19. By May 27 he was found at box 30, and on the 29th return female, 21212, came to him here, so he was polygynous. He was active at both boxes, although less so at box 25 after June 23 when he was caught there. On June 25 he was captured also at box 30. On June 29 a calamity occurred at box 25 when the young birds and nest-lining were torn out of the box onto the ground below by another wren. It is possible, but improbable that male, 22995, did it himself. However, it is more likely that either of two other males that appeared were responsible (30, 31). Neither of these other two males stayed very long, due partly to their capture and possibly in part to competition with 22995. This bird's young at box 30 left July 8, and both adults disappeared with them.

Territory No. 30.—Male, 57782, appeared June 28 at box 11 and may have sought to include box 25 (29) also in his new territory. On July 8 a female, 6891, who deserted box 40 (34) when captured on June 28, inspected box 11 but was caught and did not stay. The male shifted to box 25 on July 11th, was caught there on the 13th, sang all day the 14th, then disappeared.

Territory No. 31.—Male, 57759, was caught at box 25 on July 1. He stayed and sang around box 25 a few days more, then shifted to box 53 where he found a female and raised a brood.

Territory No. 32.—Male, 57783, who had been caught singing at box 53 July 3 and then left, showed up at box 25 at least by July 17 along with female, 26551, a return nestling, and together they raised a brood by August 20. Thus at box 25 during the season appeared in order the following males: 22995 (29), 57759 (31), 57782 (30), 57783.

Territory No. 33.—Male, 6888, was at box 75 by May 14, and a female came here by May 25. The female was found dead on the nest the second day of incubation, June 6. The male then removed the lining and another female, 6887, inspected the box on June 9. Both were caught, and this interfered with the normal progress of their nesting. The male decreased his activity, and the female did not reappear until June 12. She laid an egg on the 15th and deserted. The male must have been around, although he was not noted as very active until the 19th when he was again singing. On June 22, a female wren laid another egg, the first one still remaining in the nest. The new egg was different in color, being nearly white, so the two females were not certainly the same. On June 23, another egg was laid, but that was all. The female, 6887, was recaptured two times afterwards, but the fate and number of young, if any, is unknown. Possibly the young did not hatch or survive. The female was last caught on July 8 and on July 9. The male shifted to box 37 and obtained female, 6891, who had inspected box 11 (30) the day before and whose former mate at box 40 (34) had disappeared with their young. They raised a brood by August 12.

Territory No. 34.—Return male, 26546, was at box 40 by May 25, and possibly had been at box 37 as early as May 10. New female, 6891, came to box 40 on June 1, and their brood left on July 8. On June 28 both adults were caught at the box. Possibly the female deserted, as on July 8, the day their young left the box, she was caught inspecting box 11 (30), but did not stay. On July 9 she was back at box 37, mated with another male, and there she raised a second brood (33). Her desertion of box 40 left the male to care for the young alone, and consequently forsake his territory, which in turn allowed this new male (33) to come in and take possession of box 37 and 26546's former territory.

Territory No. 35.—Return male, 48785, appeared at box 47 by May 10. A female, 6884, was here by May 27, and their first brood flew July 3. The male did not help with the young, as the next day the old lining was removed from the box. Another female, 6885, whose brood was destroyed at box 25 (29) on June 29 and who had inspected and been caught at box 53 (27) on July 1, appeared and started a new nest-lining. On July 8 she had laid 3 eggs, but 2 were broken and discovered outside the box. She was caught and deserted the nest. She remained in the vicinity, however, and on July 15 started re-laying. Their young flew August 14. The male may have been the one heard singing around box 75 July 23 and 24.

Territory No. 36.—Return male, 26600, was at box 51 by May 17 with female, 6882. Their brood left June 27. On July 4 the male was back with a female, but they chose box 50 instead of box 51, probably because of mouse activity at the latter box. Three eggs were laid by July 8. On July 9 there was only one egg, and the female deserted. The cause of the egg loss is not known, although when the nest was removed on the 12th a mouse was found in it. On July 12, there were 2 birds at box 51 where the mouse nest had been cleaned out several days before. This may have been the same female formerly at box 50, or more probably was 6882 who mated with male, 26600, at box 59 on July 16. She may have been looking over boxes about this time, 15 days after her first brood had flown. Their second brood left August 18.

Territory No. 37.—Return male, 26601, was at box 59 by May 10 and female, 6892, came to this box about May 31. While the female was egg-laying and incubating, the male became active at box 53 on June 6. When caught there on June 10 he returned to box 59. Their brood left July 8 and neither adult was heard of again. The male from box 51 (36) took over the box within 4 days.

Territory No. 38.—Considerable shifting of activity occurred at box 53. Return male, 26601 (37), from box 59 was active here June 6-10 but left after capture. Male, 6898, appeared and was caught on June 16, but then disappeared. Return male, 6899, from box 63A (27) was interested here June 24 to July 1 and even had a female, 6885, whose brood at box 25 (29) was destroyed on June 29, inspecting there, but both were caught and neither stayed. On July 3 male, 57783 (32), appeared and was caught at this box. He likewise left, going to box 25. Finally on July 5 male, 57759, came over from box 25 (31) and obtained on this same day female, 57799, and together they raised a brood by August 13. Probably this male included boxes 9 and 52 in his territory. The replacement of so many males at this box by others may have been due to their being frightened away by capture as well as by territorial competition.

1924

Territory No. 39.—Male, 58023, was at box 3 by May 8 and box 6 by May 21. On May 22 return female, 26551, came to box 3 and started lining her nest, but when caught on May 25 she deserted. She apparently stayed in the vicinity as two birds were at box 3 on May 27, but on the 29th they both went to box 6 where their first brood was raised to leave the nest on July 2. The male remained interested intermittently in box 3 all this time, and on June 17 he had a female visit him there, and on the 19th female, A28, started her nest-lining. However, on June 27, the first day of incubation, she was caught and deserted and was not seen again. Within two days the male threw out the eggs and very soon also the nest-lining. His activity here during July gradually decreased as he was busy at box 6. He apparently did not take much care of the young out of the nest but kept singing and active near the box. On July 14, 12 days after her young had flown, female, 26551, was back at box 6 where she raised another brood.

Territory No. 40.—Male, A22, was at box 10 by May 22 and, although occcasionally at box 11, centered his attentions around this box throughout June. On June 30 female, A47, came to him and they raised a brood during the second breeding period.

Territory No. 41.—Return male, 48785, was at box 25 by April 29. On May 17 a female was here and started a nest-lining, but it was not until May 22 that feathers were added to the lining and not until the 28th that the first egg was laid. Female, 58024, who was caught at box 75 (44) on May 17 and so probably was not the female bird at box 25, raised her brood here to leave the box by July 3. As soon as the female started egg-laying, the male expanded his territory to include box 30. By June 15 he had been to box 23, and on June 30 had a female, A87, here and raised his second brood. Through July he was somewhat active at box 30, but no longer at box 25 at all, since he did not even clean out the old nest-lining.

Territory No. 42.—Male, A13, did considerable wandering and establishing of temporary territories. His identity during May was not established, but he was probably the one at box 37 on May 7 and intermittently thereafter during the month. From June 1 to 6 he was down at box 75. Possibly he "commuted" back and forth between boxes 75 and 37 in spite of the male's territory at box 43 (44) lying in between, as after his capture at box 75 on June 6, he returned to box 37 until the middle of the month. A female visited him here on June 9, but on June 25 he had left box 37 for boxes 50, 49, and 51. On July 10 he showed both box 50 and box 51 to a female, and on the 13th female, A27 (45), was also here, but no females ever stayed, and he went through the season unmated.

Territory No. 43.—A male, A50, came to vacated box 37 on June 26 with a female. However, the female did not stay, and the male remained a bachelor, although females again visited him on July 9 and 20.

Territory No. 44.—Return male, 26546, was active around boxes 43, 43A, and 75 through May, although he gave up box 75 when he got a mate at box 43. Female, 58024, visited at box 75 on May 17 but did not stay (41). Female, A10,

first came to box 43 soon after this male and the male at box 47 (45) competed for the box (and her attentions?) on May 23. However, on June 4 she was caught at the box and deserted her eggs. By June 10 both birds had gone to box 43A and started renesting. Although on June 15 her first 3 eggs were broken and carried out, she completed the set. On July 10 both adults were captured and the female again deserted, the young later dying. Perhaps it was this male that was active at box 75 and 47 during July after 57759 (45) had deserted the boxes. On July 12, female, A10, was at box 75 and probably raised a brood.

Territory No. 45.—Return male, 57759, was at box 47 by May 7, but did not show much activity until May 28 when a female came, laid an egg the next day, and then deserted. On June 8 female, A27, came to him there and she succeeded in raising a brood by July 13. Strangely, this female also inspected box 50 (42) on July 13, and may have done so on the 10th. She did not stay as she was still with the young from box 47. Male, 57759, had been more or less active at box 75 between June 17 and 25 in the interval between A13's and 26546's occupancy of that box (42, 44). After his capture on July 4 at box 47, he deserted and went up to box 53 which was then vacant. Perhaps this is the reason for the female's interest in another male and box, July 10-13. At box 53 a female visited him on July 13. Could it have been A27, his old mate, who also inspected box 50 on this date? However, he did not start another brood.

Territory No. 46.—Male, A20, was at boxes 53 and 51 by May 7. Return female, 6882, came to box 51 May 17 and had 6 eggs laid by May 25 when she was caught at the box. This disturbed her and she was away from the box, probably not entirely, but a good share of the time until May 30, after which she incubated steadily. The eggs hatched June 10, 16 days after the last one was laid, but if the 5 days are subtracted when the female was mostly away it leaves 11 days. This is an unusual behavior. Perhaps for the period she was away from the eggs during the day she was on them at night. The young left the box June 26. The male stayed around until about June 30, then shifted over to box 68 where on July 3 he was putting in sticks on top of the nest of the birds that deserted there on June 26 (47), without bothering to remove the old nest-lining. On July 5, return female, 57799, was here in the morning, although still feeding young in box 59 (47) and with her mate still present. However, she did not stay. On July 8, his female, 6882, returned to him at box 68, 13 days after their young had flown from box 51, and they raised another brood.

Territory No 47.—Return male, 6899, was at boxes 59 and 68 by May 20. On May 30 return female, 57799, came to box 59, and their brood left on July 8. The male maintained his activity at box 68 and on June 21 had a female there, but she deserted her 4th egg on the 26th. The male threw the eggs out of the nest within a couple of days and then returned to box 59. Strangely on July 5 when the box 51 male (46) became active at box 68 the female went down to visit him and was captured there at 10:00 a.m. By 10:50 a.m. she was recaptured at box 59 feeding her young. She must have been temporarily enticed by the new male's sexual activities. Both adults cared for the young off the nest on July 8.

Territory No. 48.—Male, A15, was at box 63 by May 13 and throughout May showed some activity here in singing. On June 11 he was caught at the box, so during the next few days he transferred to box 63A. Although often singing nearby, he was not active at box 63 again until July 16. The next day return female, 57799, nine days after her young left box 59 (47), came to him here, and they succeeded in raising a brood.

1925 (Figs. 7, 8)

Territory No. 49.—Return male, 58023, was active at box 3 by May 5. By May 18 he had return female, 6892, and on June 25 their brood left the box. The male had been more or less active at box 6 since June 15, so that he cared for part of the young from box 3 in the vicinity of 6 until about July 6. On this date female, 31917, came to him there and they raised their second brood by August 10.
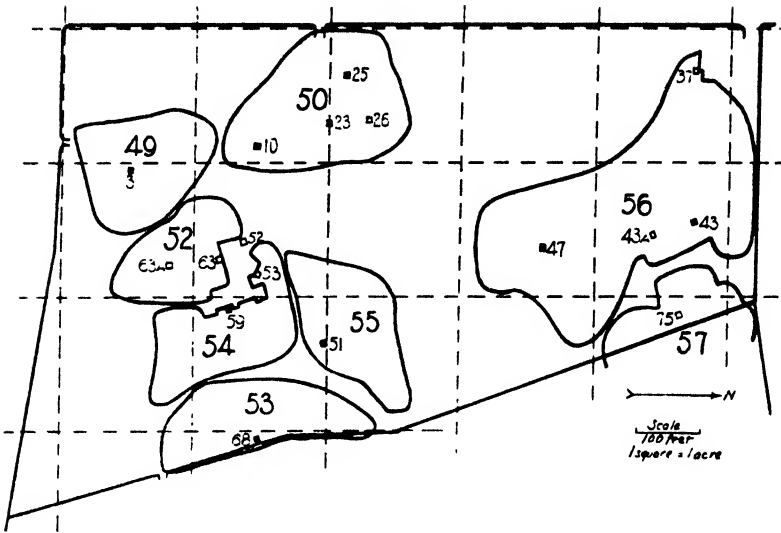
FIG. 7.—Map of territories for the first breeding period of 1925. The areas enclosed within the irregular boundaries are the territories, each one being identified by a number which refers to the case history where detailed information may be obtained. Boxes marked as solid squares are those where the males succeeded in getting mates and starting to nest; others marked as hollow squares are accessory boxes claimed by males. The grid of large squares is to aid in locating the territories by reference to Fig. 3.
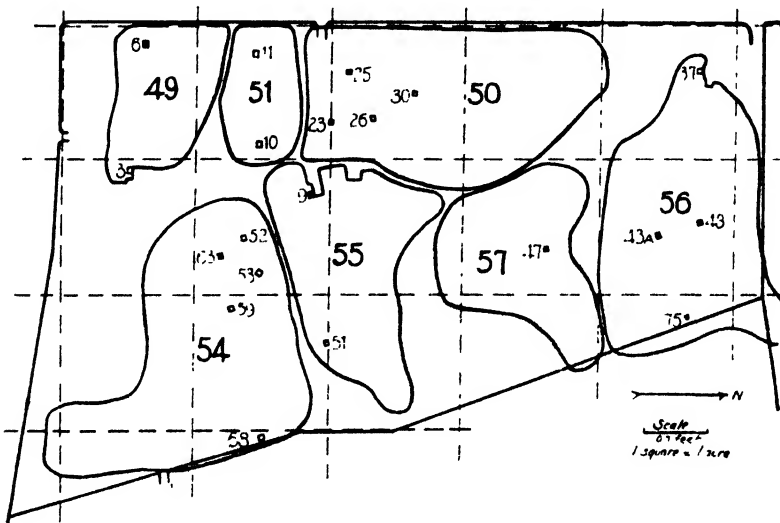
FIG. 8.—Map of territories for the second breeding period of 1925

He was more or less active around box 3 until the middle of July, but thereafter he stayed with his brood at box 6 and aided in their care out of the nest until about August 24.

Territory No. 50.—Male, A154, was at boxes 23, 25, and 26 by May 5 and at 10 by May 6. On May 19 a female, A173, came to box 25, and their brood left June 21. Meanwhile on May 29 female, 167, caught in the greenhouse the day before, came to him at box 10 and started another brood for this polygynous male. However, when both adults were caught at box 10 on June 9, they both deserted. On this day the young at box 25 hatched, and the male returned there. The male did not aid in care of the young when they left the box, but stayed singing near boxes 25 and 30. His same female, A173, came back to this territory on July 3 or possibly as early as July 1 and 2 for occasional visits and may have inspected box 30, but chose box 25, and their second brood left August 9. Both adults cared for the young until about August 21.

Territory No. 51.—An unknown bachelor male came to boxes 10 and 11 about June 26. He was mostly active at box 10 where the box 25 male (50) had deserted on June 9. A female was around boxes 10 and 11 on July 17 and 19 but not to stay, and he did not raise a brood. He left early in August.

Territory No. 52.—Male, A61, a young bird of last year, came to box 63 by May 5 and to box 63A by May 13, displacing sparrows that had started to build a nest. A female was around and probably inspected both boxes May 13 to 15 but did not stay. The male was not very active. On June 12, female, 153, who was forced out of box 68 (53) the day before, inspected box 63A, was caught, and did not stay. By June 27 the male's activity at box 63A largely ceased, and on July 2 he was caught at box 63. His territory is indicated only approximately. On July 3, it was probably he that sang here all day, stimulated perhaps by the new male, 31852, who had come to nearby box 59 (54). On July 4 both males had a female inspecting box 52, but she did not stay. Then both males disappeared as A20 took possession (54).

Territory No. 53.—Return male, 6899, was at box 68 by May 5 and female, 153, came the next day. Four eggs were laid by May 18 when the box was accidentally knocked down. It was not replaced until May 21. The adults had apparently remained nearby, as they started renesting at once. On June 7 the male was found dead, cause unknown. His territory as marked is only approximate. The female continued incubating until June 11 when a new male, probably A20, appeared singing. Perhaps the female did not want to go it alone nor the male want a ready made family, anyway they, or perhaps he, cleaned the house of all eggs and lining. The female went next day to box 63A (52) but did not stay, probably frightened by being captured there, and she disappeared from the place. The male returned to his duties at box 59 (54) and did not stay longer at box 68 without a female. A mouse occupied the box the latter half of June, although in mid-July a male was here occasionally.

Territory No. 54.—Return male, A20, came to box 59 four days after a robin's nest was removed from the top of the box. Perhaps he was aroused to nesting activity by the appearance on the same day, May 25, of female, A183. On June 11 he had an adventure at box 68 (53). His young left June 27 with him taking care of part of them. Within 3 days after his leaving, male, 31852, coming up from box 75 (57) where he had not succeeded in getting a mate, appeared at box 59 and for the next couple days there was some dispute between the two males for possession of the box, although A20 had to divide his time and attention with caring for his young. By July 4, perhaps it was 31852 from here and A61 from box 63 (52) who were competing for a female at box 52, but after that A61 disappeared and 31852 went to box 47 (57) as A20 returned. Although A20 and 183 were still occasionally with young until at least July 6, 9 days after they left the box, possibly she was the female at box 52 on July 4. Certainly the male was active at box 53 on July 5. He had a female, probably A183, around here from

July 5 to 8. However, on the latter day both shifted to box 63 where the male had also been active singing. Here they raised their second brood, which flew August 14 and was probably cared for chiefly by the female.

Territory No. 55.—Return male, 26523, appeared at box 51 by May 5 and centered his activities mostly around here during the first breeding period. On May 15 return female, 26551, came here, and on June 27 their first brood flew. The male cared for part of the young out of the box, remaining for the most part in the vicinity of box 51. An unknown male was active at box 9 from June 24 to 30 but then left. On July 3 male, 26523, from box 51 came to box 9 and on the 5th his former female, 26551, came to him here. On July 30 the male was caught at the box and deserted. The female raised the young that left the box August 11.

Territory No. 56.—Return male, 57759, was at box 47 and probably box 37 by May 5. Possibly a female inspected box 47 on May 13, and return female, 6891, was here May 19. Their brood left on June 26 and was partly cared for by the male. Meanwhile, the male was active at box 43A by June 10. The next day, or perhaps even on the 10th, a female was inspecting the box here. The male was caught at the box on the 11th. On the 12th both the male and female, A167, who had deserted box 10 (50) on June 9 at capture, transferred to box 43 where a brood was started. The female had first inspected box 75 (57) on June 11 with another male. The young hatched July 5. For the first half of July the polygynous male was mostly absent from box 43 since he was helping with the young from box 47 and was also active at boxes 43A and 37. Between July 3 and 6 it may have been he who had a female around box 75 but she did not stay. This female may have been No. 6891, his former one at box 47, for on July 6 she returned to that box and to a different male (57). The attraction of the old box was apparently greater than her previous mate. Male, 57759, after the female left him at box 75 on July 6 went to box 37 July 8-12 and even had a female visit him there on July 9, but again came back to his brood at box 43 on July 17 after his long desertion, and on the first day he took part in feeding of the young. On July 18, he was feeding them more frequently than the female and at the same time attempting to court her as a new female with song and action. Their young left July 19 with the male taking part of their care, although also somewhat active at box 43A. On July 26 he had his former female, A167, back at box 43A, 7 days after their young flew, although he continued part time with young until July 29 at least. The male deserted box 43A on August 6 and the female deserted August 17, three days after the time her eggs were due to hatch. Only a few hours after she left, one of the eggs did hatch in the heat of the sun. The delay of hatching was caused by an experiment conducted here.

Territory No. 57.—Male, 31852, was at box 75 by June 9 and had females visit him on June 11 (A167?) and on June 18 to 20. Later in the month, the male left this box and went up to boxes 59 and 52 (54), but meeting considerable competition there he came back to box 47 about July 4. Here he succeeded in wresting away part of 57759's territory (56) and even obtained that male's former mate, 6891, at this box. Their brood left on August 11, cared for by both adults.

1926 (Fig. 9)

Territory No. 58.—Return male, 57759, was the first bird to stay on the farm, May 2, although a few days before a non-singing bird was here temporarily. This May 2 bird actively gave a territory song west of the greenhouse. On May 4 he was scouting around, inspected box 26 and also the greenhouse where he was caught. By May 14 a female inspected box 25 but did not stay. The male was active at boxes 25 and 11, although on the 18th a singing male south of the main house may have been he. On May 24 a female came to him at box 25 but may not have stayed. A female was here on May 29 and returned to stay on May 31, but on June 9 she died a natural death, the day the 6th egg was due to be laid. The male had no more activity at this box. Before this happened the male had ex-

plored box 6 on May 27 and box 10 on May 28. During most of June his activity centered around boxes 11 and 6, although he investigated box 3 on June 18. On June 17 a female inspected box 6 but did not stay. On June 25 another one inspected the box and on June 27 either she or another female began carrying in lining for a nest. However, on the 28th the female, 38446, transferred her attention to box 11. Here she raised her young to 6 days of age and then deserted. The male continued his activity at both boxes 6 and 11, the former at least to July 17, but after the 25th he had to raise the young at box 11 alone. They flew on August 5. On July 28 a strange female was around and the male visited box 23 with her. On the 29th she came around box 11, probably attracted by the male's scolding, but he payed no such attention to her as he had the day before. This may be due to the fact that on the 28th while the young and nest and box were removed to dry out after they had been drenched by a heavy rain, the male reverted to his territory song near box 6 and other parts of his area. When the young were replaced later in the day he was called back to their care by my squeaking and discontinued his territory song. After August 5 he wandered away while caring for young.

Territory No. 59.—Male, A34236, arrived on the place May 6, singing between the greenhouse and the main house and later near the garage. On May 7 he roamed between boxes 53 and 80 and was caught at a banding station near box 80. His song did not seem to be as complete or as vigorous as later in the season. From May 8 to 14 he kept pretty much between the front lawn and the southeast corner. He had some nest-building activity at boxes 70A and 80, but between May 14 and 24 he was not in evidence and may have gone across Mayfield Road to a neighboring estate. By May 24 he was again active at box 70A and also began activity at box 59. The next day, the 25th, he was also at box 53, and on the 27th he came to box 51. On the 28th a male bluebird had begun nest-building at box 70A but was found dead in the box with the back of the head and neck greatly bruised as by a bird. I believe this male wren killed it but have no evidence aside from the fact that in more certain cases of murders by wrens the wounds have been similar. At any rate the wren did not keep possession of the box and two days
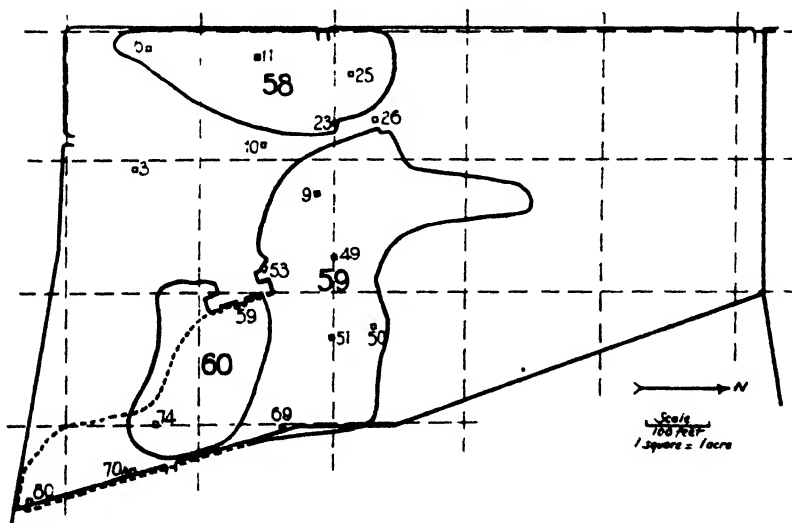
Fig. 9.—Map of territories for the whole breeding season of 1926. Where territories are indicated to be overlapping, actually one male has taken over a portion of another male's territory. The boundary of the territory that has been relinquished is shown by a broken line.

later sparrows began to build there. On May 28 he returned to box 51 and also went to box 49. On the 30th a female inspected both boxes 53 and 49 (possibly also box 51). The next day she was observed near box 49 but was not very active. However, she seemed definitely interested in the male and this box, and the male confined himself mostly to its vicinity, giving up boxes 59, 53, and 51. On June 3 the female, 63810, started her nest-lining. The male soon became involved in territorial behavior elsewhere. On June 12, a new male arrived and started to carve out a territory (60) on the front lawn, centering at box 59. Male, A34236, from box 49 gave chase, as this whole area to the southeast corner had formerly been his "tramping ground." This competition lasted for 5 days, or until June 17, and it was especially keen because a female was around and had inspected box 59 with the new male on the 13th. On June 15, the new male went down to box 69 and started tearing out the nest of bluebirds whose brood had flown June 9. Two dummy eggs were inserted to see what would happen. They were thrown out the next day. The new male was captured and banded here in the morning of the 16th. This may have disturbed him; at any rate, he made no further attempt to hold the box but retired to box 59. The male from box 49 then filled box 69 with sticks in a formless mass and with the entrance pretty well clogged. The two males had now pretty well divided the front lawn between them, and strife largely ceased after June 17. The male from box 49 continued his activity at box 69, and on the 28th a female came to him there and laid a set of eggs. Meanwhile at box 49 the female had been attending to her duties. Her young hatched June 26. The male aided her in feeding them until the female came to box 69, but after that in decreasing amounts until he had mostly deserted her by July 3. The female at box 49 now went as far west as the water tower and into the maple grove for food for the young, although the male at that time had not, as far as I could tell, incorporated this area into his territory. Later on, however, when he had a second brood at box 9 he did so. The female did not obey territorial limits, as she could not enter another bird's territory in this direction this side of No. 58. On July 5 a strange unknown bird, probably a male, came to the box, looked in, and left when he saw it occupied. He did not sing. On July 7 a male came again, this time more obtrusively. He sang repeatedly, got both himself and the female very excited, and attempted copulation with her at least three times, of which twice he may have succeeded. The male from box 59 got interested and came down to investigate, but did not stay. Male, 34236, however, was not seen. The strange male did not stay, although he was active for a few days at box 9 carrying in sticks. The female at box 49 left with her young on July 11. Strange things happened on July 11, although not related to the young leaving from box 49—more probably related to the coming in of a new female, 71653. Male, A34236, took her to inspect box 53 early in the morning, although she did not stay. This male still had young in box 49 at that hour, eggs in box 69, and was simultaneously attempting to get a new mate here. This is probably the nearest approach to a male having three females at the same time of which we have record. The male became active at box 9 adding it to his territory and carrying in sticks. On July 12 he investigated box 50. On the 14th a female was observed still around box 53 and on the 15th both male and female were at box 53, but then transferred to box 9 and started nesting at once. With the male interested in this new female he lost interest in his female at box 69 in the same manner he previously had lost interest in his female at box 49. On July 12 two eggs were missing from the 6-egg set at box 69 and on the 14th another egg was gone. The female deserted presumably due to the loss of eggs and also because of an experiment performed here on the 13th. Quite possibly the male removed the eggs in an attempt to prepare this box for the inspection of the new female mentioned above, although after the female chose box 9 he was no longer observed at box 69. His story is not yet complete. On July 22 when his box 9 female was incubating, 63810, his former mate at box 49, again made her appearance, 11 days after her brood had flown. She inspected box 51 with him and chose to stay.

By August 11 her eggs hatched while the young in box 9 were 7 days old. The male was never observed helping to feed the young in box 9, although he would sing nearby and alternate back and forth between boxes 9 and 51. On this same day he deserted his territory entirely. Once the male from box 59 came down and even looked into box 9. The female at box 9 had her brood leave on August 19, but the female at box 51 had her 6-day young destroyed on August 17, possibly by a black snake.

Territory No. 60.—This male, 63751, did not come in until about June 12, and then he was forced to compete strenuously for possession of the southern half of the front lawn with the male from box 49 (59) who had possessed the whole territory from the flower garden to the southeast corner. Perhaps a female came with him, as one inspected box 59 on the 13th. On the 15th and 16th he was at box 69 cleaning out a bluebird nest where the young had flown and removed two dummy eggs that I had inserted. He deserted the box after being captured there. On July 3 he had a female, 38479, at box 59, and their young flew August 11. At the time, the male did not have another box in his territory, so he frequently made quiet scouting expeditions to other areas. On July 5 he was once noticed coming down from the water tower, and he once looked in at box 49. Also he may have been the male driven away by the bluebirds at box 70A on this date. Box 74 was erected on July 22 after a new male was heard singing near the old tennis court. This new male immediately took possession, although for the next couple of days he was forced to compete strongly against the box 59 male for its possession. Perhaps he lost out and discouraged by the lateness of the season he left on the 26th. On August 11, when the box 59 brood flew, 63751 looked in on box 9. In both this case and earlier at box 49 his visits to other boxes occurred when the females there were alone with young, deserted by their mates. He cared for part of the young out of the box, keeping them mostly within the limits of his territory and continued to sing occasionally until August 21, after which he and the young drifted away.

1927 (Fig. 10)

Territory No. 61.—Male, A93433, was first seen at box 53 with a female on May 21. He was captured here on May 30 and deserted. The box and territory were claimed by the male at box 59 (64). He then appeared to shift to box 70A by June 8, with the male at box 74 (62) probably offering some competition. On June 10 he had shifted to box 80 and had a female. On the 14th when her 3rd egg was laid the eggs and part of the nest-lining were found gone. There were two birds here, perhaps one a new female which so excited the male to prepare a nest for her that he destroyed his own eggs and established a nest. She or some other female, A94233, was not here to stay for certain until June 19, and their brood left July 25. Box 80A was erected on June 28, and the male had some activity here during July. The male left the vicinity of the box by July 26 or 27.

Territory No. 62.—Male, A93419, along with a female, was at box 74 on April 29. On May 4, a female, possibly A94201, was here to stay, and their first brood flew June 27. During early June this male was active at box 70 and probably competed with the box 80 male (61) who came to box 70A on June 8. At box 70A both wrens gave way to sparrows which started to nest, but when I destroyed their nest, male, A93419, returned to box 70A by June 22. I purposely closed the entrance here to stop the wren from building. On July 16 with the entrance re-opened bluebirds started to build but soon abandoned the attempt, possibly due to competition with the wren as he was observed at the box a few days later. Meanwhile the male had remained active at box 74. Return female, 63810, whose first brood left box 59 (64) on July 3, was here, July 1-3, inspecting the box and even starting a nest-lining, but deserting on the 3rd when her young left box 59. Female, A94201, returned on July 7, 10 days after her first brood had flown, and she raised a second brood by August 12.

Territory No. 63.—Male, A38398, a return nestling, was at boxes 6 and 11 by May 4. On May 9 he and a female, A93420, were captured at box 6. The male disappeared. A new male, A94242, came to box 11 on this same day and had female, A93420, here by May 14. Their young left on June 30. On June 11 the male became excited by the presence of a new female and became active at boxes 3 and 6, the female choosing the latter box and starting her nest-lining on June 15. The male paid no further attention to his female and young in box 11. However, the new female at box 6 soon left, and the male tore out the lining on the 19th. On June 20th female, A94248, appeared at this box and their young flew July 27. The male remained singing at box 6 and occasionally entered the box until August 19. The female, although still with young in box 6, inspected box 53 (64) on July 25 and later visited box 30 (68). She laid her first egg at the latter box on July 30th but continued care of her brood from box 6 until at least August 2, the day her 4th egg was laid in box 30.

Territory No. 64.—Return male, A34236, was near boxes 51 and 59 by April 21 and at boxes 68 and 69 on April 27. He had no further activity at the latter two boxes, as on April 29 bluebirds started to nest at box 68. By May 4 he was at box 63 and was sporadically active there throughout May. On May 7 he was caught at a banding station near the lower windmill. On May 8 a female was with him near box 59 but return female, 63810, did not come to stay until May 23. Their first brood left July 3. From June 22 to 24, male, A34236, was active at box 53. On July 6 a female came here, and he had to compete with the male from box 51 (65) for her. She did not stay. On July 8 he was singing near box 63, but on the 10th had a female come to him again at box 53. On the 12th he had another female start at box 59. However, neither was successful. On July 13 or 14 the female was frightened away from box 53 and the two eggs later destroyed (by the male?) probably because of my disturbance and possibly because of lack of attention by the male. On the 15th his box 59 female also deserted two eggs. These eggs placed in an incubator proved infertile. From July 16 to 25 he transferred his activities to box 3. On the latter date he went back to box 53 and box 59 where the female from box 6 (63) inspected the former box and probably also the latter. He remained more or less active until August 6.
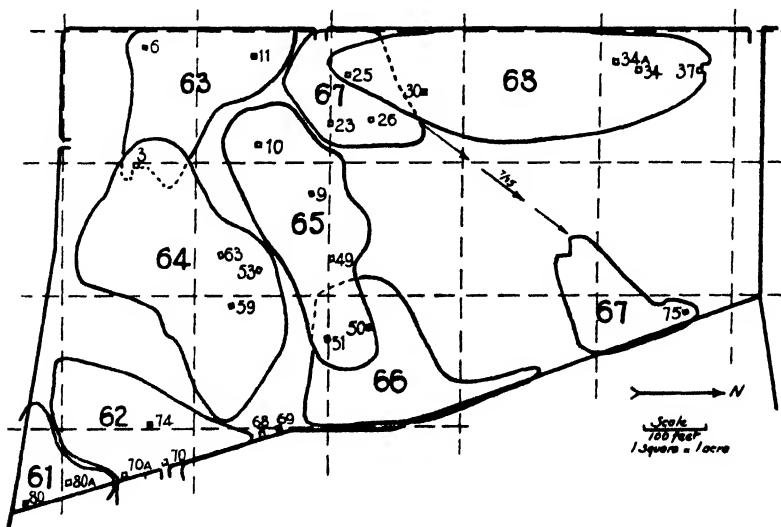
FIG. 10.—Map of territories for the whole breeding season of 1927. Territory 67 is unusual in that the male gave up his territory around boxes 23, 25, and 26 on July 15 to establish a new territory around box 75.

Territory No. 65.—Male, A94249, was not evident until May 23 at box 9, May 24 at box 49, and June 2 at box 10. On June 16 a female inspected box 9 first, then box 10, but did not stay at either place. On June 27 female, A94247, first came to box 10 but was disturbed there and transferred to box 9 the next day. She raised a brood by August 5. On July 4 the day his female at box 9 laid her 4th egg, the male went down to box 51, probably because a female, A93513, was around there. This female had had a successful first brood on another estate, had even had a new nest elsewhere with lining on June 30, but was caught, transported to the laboratory, and released on this date. She did not return to her own nest but was seen at box 51 on July 5 and had her first egg there on the 6th. When this egg was broken she wandered up to box 53 and created a squabble between A94249 and the box 59 (64) male. On July 7 she was back at box 51, laying her second egg. Possibly the laying urge prevented her from deserting the nest, and her brood left August 7. Thus this male was polygynous. For a time he appeared to aid both females in feeding the young, but he deserted both early during the first week in August.

Territory No. 66.—Male, A94202, was at boxes 50 and 51 May 4, and a female inspected box 50 the next day. On the 9th, female, A93418, was caught at box 50 and deserted, this not certainly the same bird that was around on the 4th. On May 23 a female came here again but was accidentally killed during the incubation period on June 7. The male tore out the old nest-lining here on the 9th and 10th, but beginning on the 7th he was more active at box 51. On June 22 a female inspected this box but did not stay, possibly continuing on to box 23 or box 53. By July 1 the male had left entirely and established a new territory across Mayfield Road on a neighboring estate. Why did he leave?

Territory No. 67.—Male, A94222, was at box 25 June 17-20 and at box 23 on the 20th. On the 23d a female (from box 51?) inspected box 23, but did not stay. On June 27 the male came to box 26. Another female came to box 23 on July 3 but deserted her second egg on July 5. The male remained more or less active between boxes 23 and 26 throughout June and until July 15 when he gave up this territory and established a new one at box 75 where he remained until August 10.

Territory No. 68.—An unknown male came to box 37 by June 15 and to boxes 34 and 34A by June 18 and 19 but was not very active at the boxes. On July 25 female, A94248, accepted box 30 with this male, although she had to continue care of young from box 6 (63) until August 2, the day she laid her 4th egg in box 30. The male deserted about August 14, but the female was still caring for her 15-day-old young in this box on September 1.

Territory No. 69.—New male, A93633, was active at box 75 June 22 to July 2 only. Perhaps he was an immature non-breeder with a first splurge of reproductive ardor. His territory was not mapped.

Territory No. 70.—An unknown male was at box 3 from May 29 to June 8 and then apparently shifted across Mayfield Road to a neighboring estate.

1928 (Fig. 11)

Territory No. 71.—Male, B45320, was at box 80A by May 17 and female, B45321, was here by May 25. On May 26 the male had to defend his territory and his female from the male in territory No. 72 (not mapped). On May 27 the female was captured, banded, and deserted. The male then shifted to box 80, and a female was here June 16 but deserted on the 17th. Was this the same female? The male of territory No. 72 after inspecting boxes 70 and 80A came to box 80 on June 30 and was caught, banded, and deserted. Male, B45320, returned the next day and got female, B45536, on July 6. Their brood flew on August 9. This female had been released at the laboratory after being transported on June 30 from an outlying estate where she had a brood of young. The male's territory probably extended across the road.

Territory No. 72.—On June 1 a male wren, probably 664716, was observed destroying a nest of a black-capped chickadee in the ice pond woods. Later in June he was active at boxes 70, 80A, and 80, perhaps excited by a female there, took possession away from the male (71), but was not able to keep the female. On June 30 he was caught at box 80 and either left on his own accord for the ice pond woods or was displaced by the male in territory 71. In the ice pond woods a few days later, he obtained female, B45516, in the former chickadee's nest-site who had a first brood fly from a box on the next estate June 29. Their second brood flew August 11.

Territory No. 73.—Return male, A93433, was at box 74 by May 3. A female, B45349, was here by May 21, and their first brood left June 27. The next day the male became active at box 70. On June 30 male, 664716 (72), inspected the box and tried for its possession but failed. A female was also at box 70 on June 30 to stay, which may have been the attraction for 664716. On August 8 the young left box 70. The female was banded, but was not caught for identification. Since all the banded females on the place were accounted for during the second breeding period except B45321, who deserted box 80A in May, it may have been she.

Territory No. 74.—An unknown male was at box 3 by May 12 and box 3A by May 30. Not getting a female here he became active from June 17 to July 10 at box 10, formerly occupied by the male of territory No. 75. Although a female inspected box 3A on June 28 he never succeeded in getting a mate, and when male, A94249, terminated his nesting at box 6 (75) on July 15, he was displaced from box 10 and was no longer recorded.

Territory No. 75.—Return male, A94249, came to box 11 by May 10. On May 21 he had a female, but she deserted her 6 eggs May 29. Meanwhile the male had been active at boxes 6 and 10. On June 15 he got female, 664751, at box 6 and on July 1 obtained female, B45350, at box 11, the latter having a first brood to fly from box 47 (79) on June 27. This is a short interval between nestings, but possibly she deserted when caught on June 25, or perhaps the male cared for the young out of the nest a few days longer. The young at box 47 did not leave until they were 17 days old, about two days longer than usual. On July 10 female, 664751, was caught at box 6 and deserted. The male tried to continue care of the young, which were then 6 days old, but by the 15th they had all died. He immediately transferred his attention to box 10. On July 16 female, 664751, was looking for another mate, so he showed her box 23, really outside his territory and in the area formerly defended by the box 25 male (76), but she did not stay. On the 17th she accepted box 10; thus the male again had two nests going simultaneously. On August 7 the female, B45350, was caught at box 11 and deserted Male, A94249, continued their care alone, as they were 11 days old, and was also active part time at box 10. On August 10 he was captured at box 10 and thereafter spent all his time with the brood at box 11, which flew the next day. On August 17 the female deserted the single remaining young bird in box 10 after she was captured. So with all his effort this male succeeded in raising only one brood during the entire season.

Territory No. 76.—Male, 664601, was at box 30 by May 9, at box 26 by May 12, and box 25 by May 13. On May 14 return female, A93526, came to box 30, but when caught she deserted. On May 16 she settled at box 25, but was accidentally killed on June 22, so that the male cared for the young alone and brought them off June 26. Before the female's death the male had returned for activity at box 30, and had extended his territory to box 23 and on east of the laboratory. On July 6, 10 days after the young had flown, the male was active again at box 25, and on the 9th a female came to him at box 30. She deserted on July 29 when her eggs failed to hatch.

Territory No. 77.—An unknown male was at box 63 by May 15 and had a female here May 21, but she died egg-laying on May 26. By May 30 he had gone to box 59. On June 11 he had a female here, but when one of her eggs was

broken (accidentally?) on June 21 she deserted. On June 16 and again on June 25 the male here had to fight in defense of his territory with the box 51 male (78) in a real battle. Perhaps this box 51 male destroyed the egg in box 59 on June 21, although there is no evidence. A singing male was near on June 27, and this may have been the box 59 male, but he disappeared the following day.

Territory No. 78.—Return male, A38398, was caught May 8 in the greenhouse and was active around box 50 by May 9, box 9 by May 12, box 51 by May 21, and box 52 and 53 by May 23. A female was at box 51 on June 3 but did not stay. On June 12-14 the uneasy male was active at boxes 53, 50, and 69. On June 16 and again on June 25 this male invaded the territory of the box 59 male (77) and there were serious fights. On the latter day female, B45348, came to box 51 after being first trapped at a banding station near the lower windmill on June 21. This female may have been the one that deserted box 59 (77) on June 21. After this date the box 59 male was no longer recorded, and a month later the male, A38398, was active at box 59. On July 29 his young flew from box 51.

Territory No. 79.—Male, A93573, a return nestling, was first active at box 37 on May 10, but when caught there on May 14 he transferred to box 47. By May 22 female, B45350, came and the male probably showed her both boxes 47 and 47A, although it was at the former box that she raised her first brood by June 27. On July 6, female, B45349, came 9 days after her first brood had flown from box 74 (73), and their second brood left on August 17.

Territory No. 80.—Male, whose identity is unknown, came to box 37 soon after May 14 when male, A93573, who was first active here (79), was frightened away. Female, 664708, was here by May 21 after the male had probably also shown her box 34. Misfortune came to their young, all but one of whom had disappeared by June 17. The female deserted on June 17 due in large part to interference from me. The male remained active until about July 25, going also to boxes 34A and 35, but he did not renest.

Territory No. 81.—An unknown male came to box 75 by May 23 and box 78 by June 9, and had female, 664708, who left box 37 (80) on June 17, at box 75 on June 22, and their young flew July 27. The male did not care for the young much after July 16, although he probably remained in the territory somewhat longer.
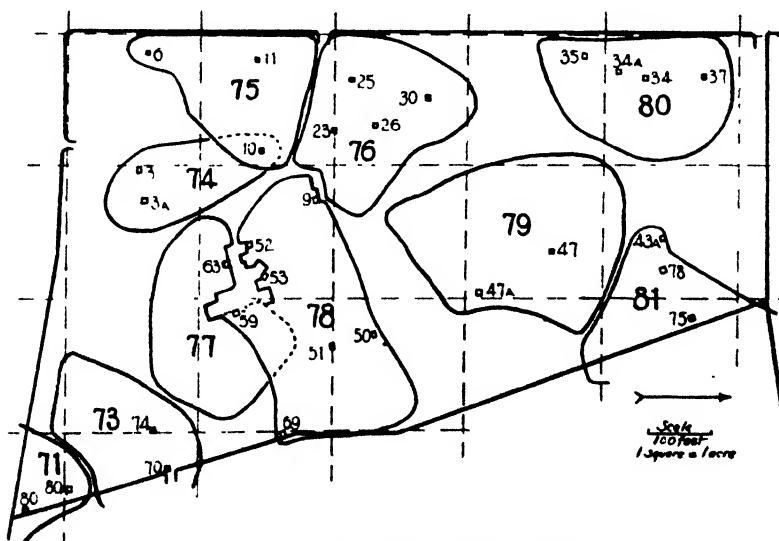
Fig. 11.—Breeding season, 1928
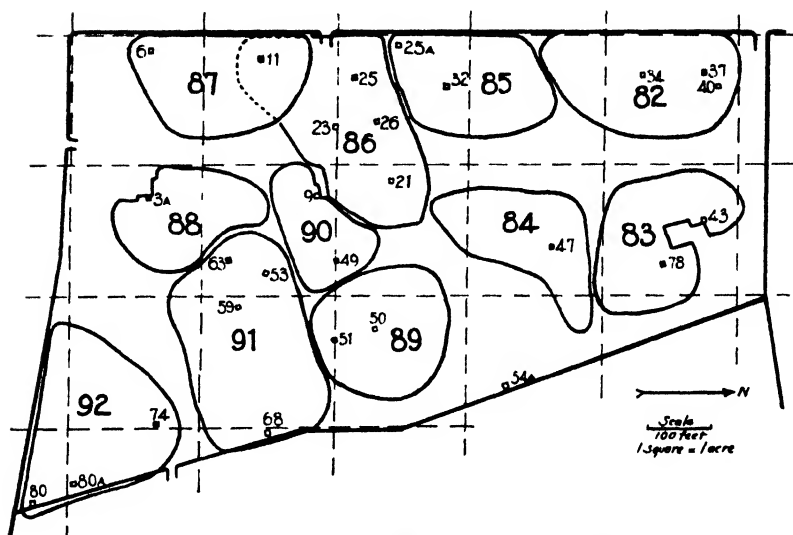
Fig. 12.—First breeding period, 1929
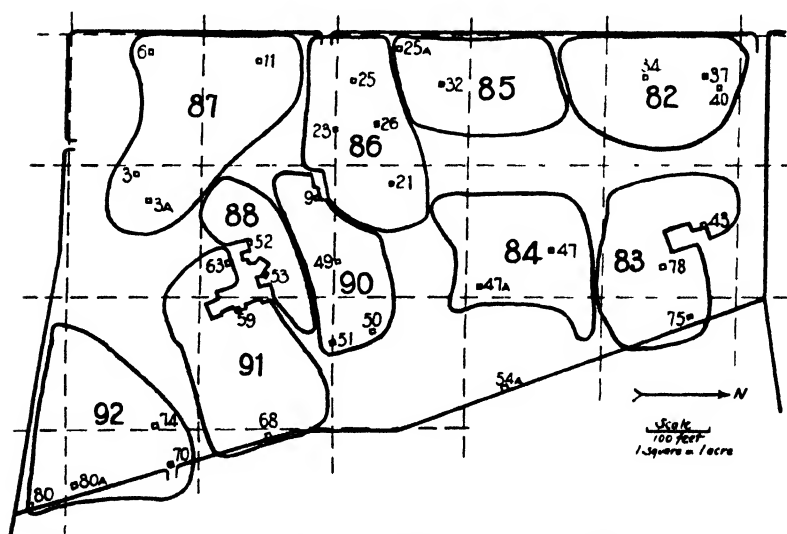
Fig. 13.—Second breeding period, 1929

1929 (Figs. 12, 13)

Territory No. 82.—Male, B97101, was active at boxes 34, 37, and 40 in May. By May 15 return female, 664708, was at box 37 (from box 43 (83)?), and on June 22 her young flew. On July 1 a female inspected box 37 but did not stay. On July 10 female, B97102, did stay and she raised a brood.

Territory No. 83.—Male, B46487, was caught on the laboratory porch May 6 and was active at box 43 by the middle of May. By May 15 a female (664708?) came to box 43 but soon deserted. Female, B96433, came to box 78 by May 24, however, and their young flew June 30. On June 22 the male was somewhat active at box 75, but not much again until July 8, eight days after his first brood had flown. He must have taken care of the young entirely after June 25 when the female was captured and deserted. Female, B96900, whose first brood at a neighboring estate had flown about 8 days before, appeared at box 75 on July 11. It is possible she deserted her first brood 13 days before when captured at the box. Her second brood flew August 21.

Territory No. 84.—An unknown male was present at box 47 by May 15 and a female here May 20, but she deserted her eggs May 24. On June 11 female, B97003, perhaps the same one as was here earlier, came again and their young flew July 16. This male was apparently kept out of box 54A by bluebirds which nested there all season. Instead he went to box 47A, where wrens were seldom seen. From July 8 to 23 he was active at this box but was interfered with by a mouse that succeeded in raising her young even though the male wren had earlier carried sticks onto the top of her nest.

Territory No. 85.—Male, B97007, was at box 32 with a female June 1. On May 24 a sparrow's nest had been removed from the box, and its presence may have delayed the wren's starting earlier to nest. On June 6 the female deserted the eggs and nest. Before June 15 the male had some slight activity at box 25A. From June 18 to 20 a female was again at box 32, perhaps the same one, although she did not stay. On June 29 female, B96433, arrived, although her first brood at box 78 (83) did not leave the nest until the next day; perhaps she deserted when captured June 25. Their young flew August 6.

Territory No. 86.—Return male, A94249, first appeared at box 11 on April 27. An unknown female came on May 14 but deserted her first egg, May 20. The male next became active at boxes 23 and 26, and when the sparrow nest at box 25 was removed on the 24th, he soon shifted over there. On May 30 female, B56490, brought in from an outlying estate on May 17, came here, and their first brood left July 6. On May 30 when the male was all excited with his new female, he apparently destroyed the eggs of a pair of bluebirds at box 21 and had some nest-building activity there. Later, during the middle of June, he was active again at box 23 for a few days, but by July 2 he returned to box 21. On July 8, two days after their first brood had flown, he had female, B56490, back at box 21, and their second brood flew August 17. Their first brood at flying consisted of only one bird and it did not interfere much in the birds' remating activities.

Territory No. 87.—Male, B96434, was not noticed until about June 1 at boxes 11 and 6. This was the time that the male in territory No. 86 was occupied at boxes 25 and 21 with a female, although he had previously been with a female at box 11. Female, B96001, came to box 11 on June 1. This female had been brought in from an outlying estate on May 27, at which time she was nearly ready for egg-laying. Their brood left July 8. By July 11 the male had wandered to box 3 and by July 16 had gone to box 3A, vacated since June 26 by the male in territory No. 88. On July 27 a female came to him there, but on August 3 she deserted her fifth egg, possibly due to the lateness of the season.

Territory No. 88.—Male, B56491, together with female, B96417, were at box 3A by May 25, but the female deserted her young, and the young died on June 26. The male was not caught at this box, but may well be the bird of this number that on

July 7 became active at boxes 52 and 53, over two weeks after the male in territory No. 91 had ceased activity at the latter box. Female, B96001, came to him at box 53 on July 9, the day after her first brood of two birds had left box 11 (87). (What happened to them?) Their second brood left August 14.

Territory No. 89.—Return male, A38398, arrived April 27 and by May 15 had return female, B45348, at box 51. Their first brood left June 23. In May the male had been active at box 50, possibly disrupting a bluebird nesting there, as his sticks were later found on top of the nest. However, he did not prevent bluebirds from nesting at box 49. The male may have helped care for the young wrens when they left the box, although there were only 3, as he was not seen again and the female was hunting a mate 4 to 7 days later.

Territory No. 90.—Male, B97018, was active throughout June at box 9. On June 4 he had to defend this box against the male from box 3A (88). After the bluebird brood flew from box 49 on June 11 the male became active there, and on June 27 a female inspected the box. About this time the male also became active at box 51 which the male in territory No. 89 had recently vacated. This female may have been the one that deserted box 3A the day before, or it may have been B45348, whose young had flown from box 51 on June 23. More certainly the roving female June 30-July 4 was this latter bird. She inspected box 9 on June 30, box 50 on July 1, box 49 on July 2, and was back at box 9 July 3 and 4 and might have stayed here except that my interference disturbed her. On July 4 she returned to box 51, and her second brood left there August 6.

Territory No. 91.—Return male, A93433, was active in early May at boxes 63, 59, 53, and 68. By May 19 he had return female, 664751, at box 63, and their young left on June 26. He remained more or less active at the three other boxes through June, but on July 1 a female came to him at box 59. Her identity is not known as she deserted her 7-day-old young, leaving the male to care for them entirely, which he did successfully.

Territory No. 92.—Male, B96418, was at box 80 by May 15; his activity there being terminated in middle June when a mouse took possession. He was not at box 80A until after May 24 when a bluebird nesting was completed. He had activity there for only a few days in early June, as by the 14th the bluebirds were back for renesting. Probably he did not defend these boxes vigorously. A return nestling of two years before, female, B5640, came to him at box 74 by May 20, and their first brood left June 26. The male then switched to box 70 on July 6, perhaps partly persuaded by a mouse appropriating box 74 on July 5. His former female returned to him on the same day, 10 days after their first brood had flown, and their second brood left in the middle of August.

1930 (Fig. 14)

Territory No. 93 —Return male, B56487, was singing in the barnyard on May 4, was at boxes 75 and 43A by May 12 and at boxes 43 and 78 by May 18. On May 13 return female, B96433, came to box 43A from box 47 (95), and their first brood flew June 20. The male did not aid in their care much after the first couple of days. He was at box 78 on June 23, at boxes 75 and 43A on June 24, and at box 43 on June 25. Female, C68705, came to box 43 on June 26 but deserted her young on July 23, probably because of my interference at the nest, and the young were placed in another box. On July 2 a female visited the male at box 78, and 2 days later even laid a first egg before she deserted. The territory of this male as originally marked included box 47, but this was later subdivided (94).

Territory No. 94.—An unknown male came to box 47 on June 20 and an unknown female on June 26. Could this have been female, B96433, from 43A (93)? They deserted their nest at hatching of the eggs due to interference. Probably C68801 (95) was the male here early in the season, but he had left this box by May 25.

Territory No. 95.—Male, C68801, was at box 47 by May 4 and had return female, B96433, here May 9, but after being captured she deserted. The male continued to be active at the box until May 25, with occasional activity also at box 47A, and perhaps was more or less around through June. The female went over to the male at box 43A (93) on May 13. Bluebirds, which had been nesting at box 54A, had their nest destroyed by sparrows, probably June 9. Male wren, C68801, came to this box July 7, and female, C68257, who had deserted box 49 on July 3 (97), came here July 9, and their brood left August 13.

Territory No. 96.—Male, C68911, was in the territory by May 12 at boxes 11, 26, and 30. Female, C68253, came to box 26 on May 15, but their young were deserted on June 7 due to my interference. On July 11 the pair was observed at box 30, but the female did not stay. On the 12th they started a nest at box 25 where the male had been more or less active since June 5. Their young left July 19, the male questionably aiding in their care. A female also came to box 6 on June 16, but eggs and nest were deserted on July 2, so this male was polygynous.

Territory No. 97.—Return male, B97018, and an unknown female were at boxes 49 and 53 by May 3. Probably this same female, C68254, remained near box 49 until May 11 when the male was frightened from the box by me, then the next day the two shifted to box 53 and started a nest. The young flew June 28. Meanwhile the male had been somewhat active at box 52, possibly once at box 21, and also at box 49, for on June 8 or 9 female, C68257, came to this latter box. Perhaps she was the female that deserted box 74 (102) on June 7 when she laid her 2nd egg. However, on July 3 she deserted box 49 after being trapped, apparently a very timid bird. The male thus was polygynous and he may have been absent with the young from box 53 at the time the female was caught at box 49. He remained active at the box until about July 15.

Territory No. 98.—Return male, A38398, arrived in the vicinity of boxes 50 and 51 by May 7, and return female, B45348, was at box 51 on the same date. Their young left on June 23. The male became active at box 50 on June 27, had a female (his old one?) here on July 3, but due to interference she deserted on July 7. The male then transferred back to box 51 on July 8; a female was here on the 11th, but no nesting was undertaken.

Territory No. 99.—A bluebird was nesting early in the season at box 3A, but on May 15 its eggs were gone, and very shortly male wren, C68800, became active
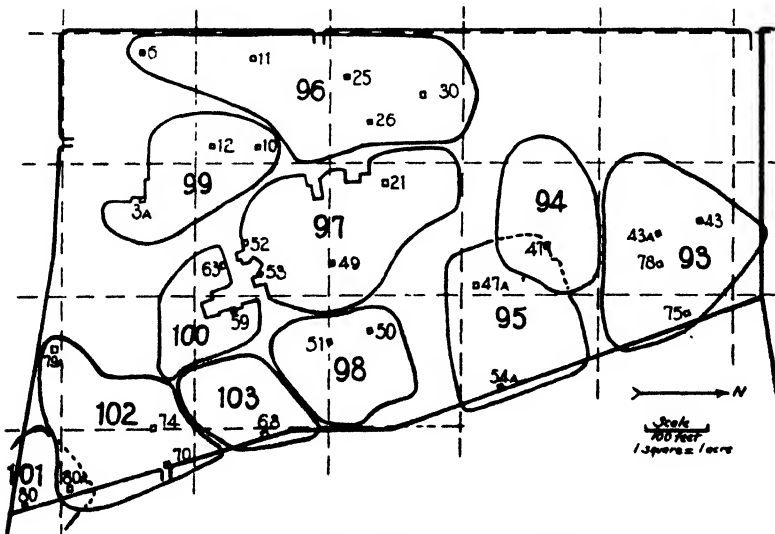
FIG. 14.—Breeding season, 1930

here. Did he destroy the bluebird nest? On May 27 a female wren was here. Could she have been the one that deserted box 80A (102) on May 23? On June 3 she laid her 3rd egg, but due to interference deserted. The male continued active at boxes 3A, 12, and 10 through the rest of June. On July 2 a new female came here but was accidentally killed. Male activity was noted until July 16 only.

Territory No. 100.—Male, C68910, came to box 59 soon after a sparrow's nest was removed on May 4. On May 22 he had return female, B5640, here, but due to destruction (by sparrows?) of eggs as they were laid she deserted on June 1. She started egg-laying again on June 6, but on the 8th the eggs were again gone. The male shifted over to box 63 for a brief time three days after this failure, but was back at box 59 on the 9th. His persistence was probably a drawing force, as the female came back a third time, assuming her to be the same bird, on June 15. Their young flew July 20, the male aiding in the care.

Territory No. 101.—Male, C68252, was at box 80A a day or so after the box 74 male (102) had been caught here and deserted on May 3. He had female, B96282, a return nestling, here by May 15, but due to my interference she deserted her 6th egg, and on the next day both adults transferred to box 80. The first new egg was laid on May 28, and the young left about July 1. The male disappeared after July 5, although he may have been seen with young July 15. The female renested across Mayfield Road beginning about July 2. It seems very probable that the male cared for the 2 young entirely. It is possible that the female deserted the nest on June 24 when she was trapped at the box.

Territory No. 102.—Return male, A93433, had a female on May 3, and they inspected boxes 80A, 74, and 70 in this order, staying at none. However, he had another female at box 74 by May 12, but she deserted her second egg May 20. A female, perhaps the same one, was nearby scolding on the 21st and inspected box 74 on the 26th, about the time the male had some activity at box 79A. The female did not stay until June 2, and on June 7 she again deserted due to my interference after she had laid her second egg. This female was probably C68257, who was caught at a nearby banding station on June 6 and went to box 49 on June 8 or 9 (97). The male paid some attention to box 70 on June 9 and was more or less active until July 7. A mouse took over box 74 on July 1, and the male finally disappeared.

Territory No. 103.—A pair of bluebirds was at box 68 until June 17 when the first egg laid disappeared and the birds deserted. There was activity at the box on June 19 and 21, either of bluebirds or of house wrens. On the 22nd an unknown male wren was definitely here. The bluebird pair returned once on the 25th, then disappeared. On June 30 and July 1 there was an intense song competition between this new male and the male wren from box 74 (102), and the stranger won out. Female, C68901, may have been the cause of it as she was caught at the box July 1 and stayed until the 5th but did not nest. The male remained active until about July 9 and may have been back July 17 but was not noted later.

Territory No. 104.—Male, B96446, was in the ice pond woods by May 12 and had female, C68563, at box 72A by May 18. The first brood flew June 27, and the male aided in their care. They remated and started a second brood at box 72B about July 19, but the young met disaster 4 days after hatching. This territory is not mapped.

1931 (Figs. 15, 16)

Territory No. 105.—On May 9 a return male, C68910, was captured at box 3A and then deserted or was replaced by a new male, later going to box 49. Male, C94215, was at box 3A by May 18 and female, C94216, was there by May 27. This male kept expanding his territory down toward the main house. On June 12, perhaps partly stimulated by the male from box 25 (106) and the presence of an unattached female from box 49 (108), he added box 53 to his area in the morning, was competing with the box 25 male at box 9 by noon, and competing with him for

part of the orchard in the afternoon. He cared for part of the young that left box 3A on July 1 until July 13, the young following him about on his territory. The female cared for the others but seemed to have a crippled leg. Neither renested. A female inspected his box 63 on July 17.

Territory No. 106.—Return male, C68801, was at box 25 by May 7 and return female, C68253, was here May 15. He was active also at box 30 about May 28, and a female visited him here June 3 and 19, but neither time stayed. On June 12 the male was caught in the morning. Perhaps this disturbed him, and in addition the female who deserted box 49 (108) was looking for a box and mate, so by noon he was competing in song with the box 3A male (105) near box 9 and in the afternoon in the orchard. From June 14 to 25 he was more or less active at box 10, which a brood of bluebirds had vacated on June 10. On June 23 his own brood left box 25. He aided the female in caring for the young but was also active part of the time at boxes 25 and 30. Beginning June 27 the female cared for the young alone, while the male remained intermittently active at box 25 until August 7 without getting a second mate.

Territory No. 107.—Male, C94194, was at boxes 53, 50, and 51 May 9 and a female was at box 53 on May 18, but she deserted her first egg May 24. The male was not heard of again. The male from box 49 (108) was at box 53 either the 25th or the 26th and may have had something to do with the female's desertion. The territory is not marked.

Territory No. 108.—This return male, C68910, was a very energetic one. He was trapped at box 3A on May 9. This apparently frightened him and he left or was replaced by the new male that came in (105). He may have been active at box 63 by May 26 but then transferred to box 49. His early temporary territory around boxes 3A and 63 is not marked. He may have influenced the female to desert at box 53 (107) on the 24th as he was active there until the 28th. On the 30th a female (this same one?) came to him at box 49 and was in the 3rd day of incubation on June 10 when my interference for an experiment caused her to desert. This male had meanwhile been active at boxes 53 and 52 but probably not at 50 and 51. On June 11 he conducted a female, probably the same one, to inspect box 51 in the morning, but she did not stay. In the afternoon they inspected box 50 but did not stay. In the evening they examined box 53 and likewise did not stay. On June 12, the males from boxes 3A and 25 (105, 106) entered energetically into the competition for territory and the female. Male, C68910, however, led the female, F45359, into an entirely new area, for on June 13 they were at box 54A to stay, replacing the male from box 47 (113) with eggs who had been active there the day before. Their young left July 18, and the male aided in their care. The male occasionally returned to box 51 for activity and singing.

Territory No. 109.—Male, B97203, a return nestling from two years back, was active at boxes 70 and 74 by May 9. On May 18 return female, B5640, came to him at box 74, and their first brood left the box June 27, the male aiding in their care. A strange male had looked into the box on June 15. The day after the young left, the male from box 80A (111) started activity here, so that when B97203 became free of young he found his territory occupied. He then went up to boxes 59 and 53, not then in use, but could not get a new mate, July 7-18.

Territory No. 110.—Until June 13 a pair of sparrows had a nest in box 59, but on this date it was removed. On June 19 male wren, F45357, came in, had to contest for the box against house sparrows, especially the female sparrow, and on June 21 was competing vigorously with the male from box 74 (109). He succeeded in wresting away a slice of that male's territory, so that by June 25 he covered a large part of the front lawn. On June 21, a return female, C68681, came to him, but on July 3 after laying her 4th egg she deserted. On July 4 the male was caught and rather roughly handled, so he also deserted. This vacated the territory, so that on July 7 the male from box 74 who formerly owned part of this territory came up and took possession.
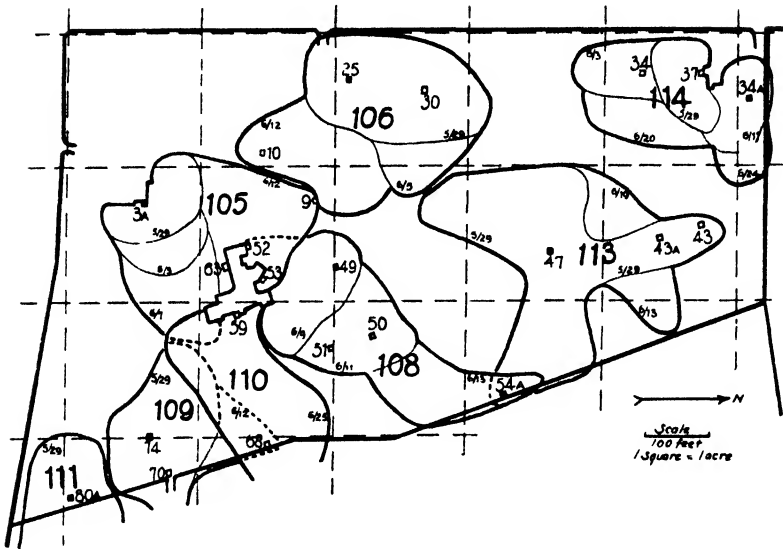
FIG. 15.—First breeding period, 1931. Progressive changes in the size and shape of the territories are indicated by light lines along with the date on which these territorial limits were first recorded. The greatest extent of the territories is shown by heavy lines. Broken lines are boundaries of areas given up by one male to another.
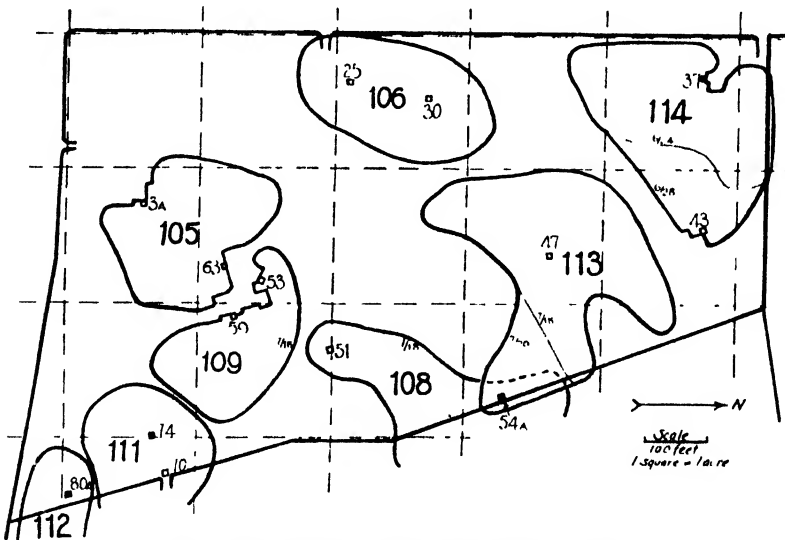
FIG. 16.—Second breeding period, 1931

Territory No. 111.—A strange unidentified male was at box 80A by May 7. On May 10 there were two male wrens competing at the box, and C68252, a return, won out. On May 15, female, C94331, came, and their first brood flew June 25. The male appeared to be taking care of the young mostly in the ice pond woods and the female was not again found. While the male was away his territory was preempted by another bird (112), and so beginning June 28 he began singing at box 74, although still obliged for part of his time to be with the young from box 80A in the ice pond woods. The male originally here at box 74 (109) was also away caring for young. On July 7 he started to spend nearly full time at the box and at box 70, partly because his young were now 12 days out of the box and possibly also because the former male here (109) was again making an appearance after caring for his young. That male, however, transferred to box 59 instead of contesting for box 74. On July 13 a female inspected box 74 but did not stay. A female stayed on July 18, and their second brood flew on August 23. Perhaps this female was the same one that visited the male at box 63 (105) the day before. The identity of the female is not known as she deserted the nest about August 15. The male had another female visit him July 29, but she did not stay.

Territory No. 112.—While male, C68252, was busy caring for his young (111) a new unknown male, possibly the one seen at box 74 on June 15 (109), took possession of box 80A on June 27, and on July 2 a female visited him there. This was probably either C94331 or B5640, although the latter was still caring part time for her young from box 74 (109), only 5 days out of the box. B5640, however, laid her first egg here on July 8, and the young died from an experiment August 11.

Territory No. 113.—Return male, B56487, was at box 47 by May 7, at box 43A and possibly box 43 by May 18, and probably box 54A by May 25. On this latter date female, C94217, came to box 47, so he mostly ceased his activity at the other boxes until June 12, the day of the intense competition around box 9 for the unattached female (108), when he became active again at box 54A. However, the next day the male from box 49 replaced him here as he was probably the more vigorous of the two, being without a nest but with his old female, while B56487 had a nest at box 47. B56487 transferred his excess activity to box 43A June 13 to 17. On July 1 his young left box 47 and he aided in their care. This male did not get a second brood, although he was active at box 54A from July 20 to 30, recapturing this former portion of his territory.

Territory No. 114.—Male, C68418, a return nestling, was active at box 37 by May 18 and had a female here May 30. She laid her 3rd egg on June 4 but not her 4th until June 7. Possibly it was because her behavior was so irregular that her eggs were destroyed on the 8th by the male. The next day the male turned his attention to boxes 34 and 34A and female, C94219, probably the same one, came on the 10th, first to inspect box 34, then to stay at box 34A. Again she laid only 3 eggs, but she raised the brood to leave the box on July 18. The male did not aid much with the young, being somewhat active at box 43 June 28 to July 13. On the latter date he transferred all his attention to box 37. Female, F45565, came here on July 15th, and their young flew August 15, the male probably aiding a little in their care. This female had a first brood on another estate, with her young leaving July 16, although probably she deserted her nest when trapped at the box on July 11.

1932 (Figs. 17, 18)

Territory No. 115.—Male, F45934, was first active at boxes 37 and 40A about May 1, but due to capture on May 10 he shifted down to box 43A and got a female, H18249, there by May 19 or before. The young left by June 25. Meanwhile he expanded his territory into the maple grove and to box 43. His attention to box 75 was not very serious as another unknown male was active here June 24-29 and even had a banded female visit him on the 29th. Either F45934 or this new male from box 75, I believe the former, was at box 43A on June 28. A female came on the 29th, but on the 2nd day of incubation the nest box was accidentally torn down.
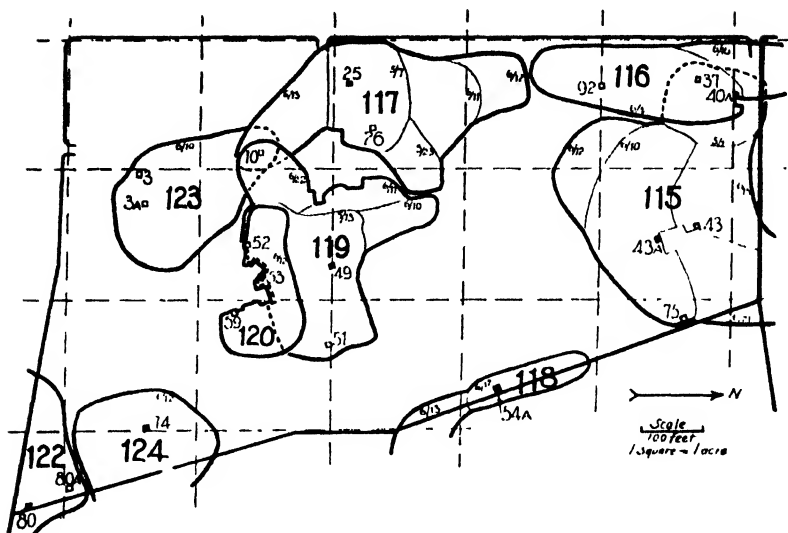
FIG. 17.—First breeding period, 1932
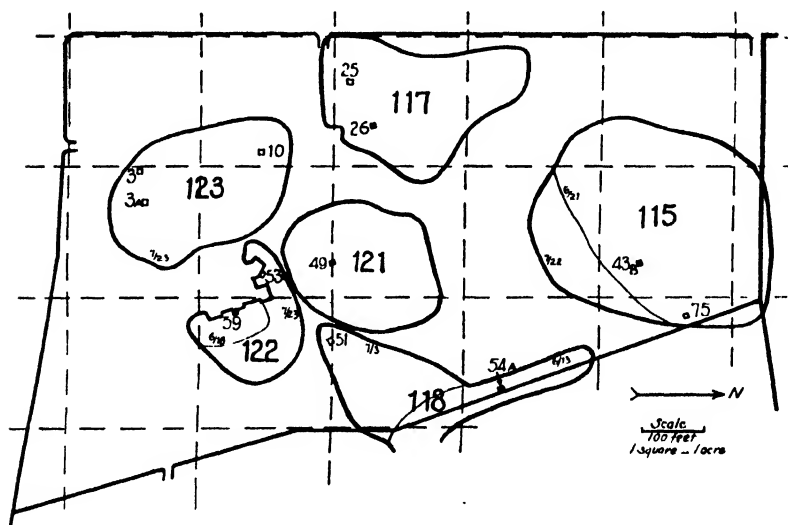
FIG. 18.—Second breeding period, 1932

The male then looked over box 75 again the next day and once went up into territory 116 where he was chased out. He settled at box 43B where female, F45945, came probably on the same day (July 11) and laid an egg 4 days after her (?) box 43A had been destroyed. The young left on August 22.

Territory No. 116.—Male, F58648, was at box 40A on May 31 after the previous male (115) had deserted. Return female, F45359, came on June 4, and on July 11 the young flew. On June 12 a foreign male (115) attempted copulation with her, but the male chased him away. From June 4 to 20 the male was somewhat active at box 92, but apparently not at box 37.

Territory No. 117.—Male, F45946, had arrived at box 25 by April 28. A female visited the area on May 7, but the male could not coax her into the box due to human interference nearby. On May 12, however, female, F45942, was here to stay, and on June 21 the young left. The male was trapped at the box on June 11. Possibly that stimulated him someway, as on the 11th and 12th he expanded his territory into the maple grove and on the 13th to box 10. He had been active at box 26 by June 4. The male may have cared for the young or part of them a few days after they left the box, but he was back at box 25 from June 26 to 29 and on the 28th and 29th had a female there who did not stay. On July 3, however, a female, probably his old one, F45942, came to him at box 26. This might have been the female to visit him at box 25 a few days previously. She deserted him and her young on August 1, so the male had to continue their care. They left on August 6. It is interesting that on this date the male visited box 25 a few times.

Territory No. 118.—Male, F45987, was at box 54A by May 24 and female, F45992, was there by May 29. Due to experimentation their first nesting was terminated unsuccessfully July 5. Between July 3 and 16 and possibly until the 23rd the male had some activity at box 51. However, on July 6 a male was also at box 54A, on the 8th a nest-lining was in, and the next day the first egg was laid, this only 3 or possibly 4 days after the first nesting was abandoned. Neither the female nor male was trapped, but probably they were the same pair that was here for the first brood, more certainly so for the female. The brood was again unsuccessful, July 28, due to my interference.

Territory No. 119.—Four males were involved in a tangle of relations and the interpretation may not be everywhere correct (119, 120, 121, 122). Return male, C68910, was active at box 49 by April 28, box 53 by April 29, box 51 by May 13 and perhaps box 52 by May 7 when a female inspected this last box. The female did not stay there but possibly the same one, F45947, stayed at box 49 on May 12 and raised a first brood by June 24. The male had some activity at box 10, but when the young left box 49 he helped to care for them and disappeared.

Territory No. 120.—Male, F45994, was probably the bird at box 59 on May 3. A female came on May 18, but their first nesting was terminated when the eggs were broken on May 29. The male remained more or less around the box until June 7, but by June 2 he was also active at box 53 and later at box 52. The male formerly at these two boxes (119) was now more interested in and confined to the neighborhood of box 49. On June 4 return female, C94219, came to box 53 four days after her nest at box 80 (122) was destroyed, and on July 11 their first brood left the box. The female died accidentally in the apple orchard two days later, so the male probably cared for the young, and he left the vicinity.

Territory No. 121.—Male, F45763, a return nestling, came to box 49 on June 29, possibly from box 75 (115) and took possession of nearly the entire territory of the former male there (119). On this date he chased out of his territory the female from box 53 (120) who was going into the flower garden for food for her young. However, on July 7 he paid no attention to that same female in his territory, as he was then trying to get a mate of his own at box 49. Female, F45947, returned to box 49, 11 days after the young of her first brood had left this same box (119). Her second brood left August 12, and the male accidentally drowned in a bucket of water at the farm-house on the same day.

Territory No. 122.—Return male, C68252, came to boxes 80 and 80A by April 28 and had a female inspect his two boxes on May 3, but she did not stay. On May 13 a return female, C94219, accepted box 80. Her eggs were destroyed on May 31 and she left. The male then turned to box 80A for his activity but left on June 2 or soon after. With the male in territory 120 withdrawing from box 59 to become active at box 53, male, C68252, reappeared at box 59 by June 18 and had a female the next day. Their nesting was interrupted on the 23rd. This same or another female tried again on June 30, but again the eggs were deserted on July 22. The male had expanded his territory to include the vacated box 53 on July 14, three days after the male there had left with young. On July 9 a banded male, possibly this one, visited box 3A but did not stay. On July 28 a female inspected box 59, but the male attempted no further nesting.

Territory No. 123.—The male here was never banded but was at boxes 10 and 3A by May 31 and box 3 by June 6. A female inspected his box 10 on June 9 but did not stay. He obtained a female at box 3A on June 20, but she died with the 5th egg in her oviduct on June 30. By July 5 he left boxes 3A and 3, and on July 6 returned to box 10 where since June 9 males from boxes 25 and 49 had been briefly active (117, 119). On July 15 a female may have visited him but did not stay, and he remained active only until the 23rd.

Territory No. 124.—Return male, B97203, came to box 74 by April 28, and a female was here on May 5. The female flew towards territory No. 122, and there was some strife in song between the two males for the female and territory. Possibly this female was the one that inspected boxes 80 and 80A on May 3 and perhaps the same one that stayed there May 13. On May 16, the male had return female, B5640, at box 74, and their first brood flew June 23. The male aided in caring for young out of the box. He returned to activity at the box on July 1 but then disappeared. A silent male was seen near the box on July 13.

1933 (Figs. 19, 20)

Territory No. 125.—Male, H18577, became active around boxes 59 and 63 late in April and early in May. On May 24 a female arrived at box 63 and laid 6 eggs but deserted them for some unknown cause on June 1. On this date the male was caught in a mammal cage nearby—did this disturb the female? This male then transferred to box 3A where the 4th attempt of a sparrow to nest had been destroyed. On June 8 the male was back with a female, H18581, at box 59, which female may have been the one that deserted box 63. Their first brood left the box July 17. There was little further activity in the territory. The male may have moved across Mayfield Road.

Territory No. 126.—Male, H18580, with female, H18583, came to box 10 by May 20. After the female was well established here, the male spent considerable time in early June at boxes 3 and 3A. On June 20 when this male was away, the male from territory No. 127 looked into box 10 and was driven away by the female. On June 22 the female deserted, possibly because of neglect by the male. The male came back to the box on this date after the female left, but it was too late. He remained on his territory until about the middle of July.

Territory No. 127.—Male, H18600, came to box 11 by May 20, possibly driving out the male from territory No. 128, formerly active near here, as that male then had a female starting to nest at box 25. A female was also at box 11 on the same date but left on May 23, when her first egg was accidentally broken. Perhaps she was F58955, return nestling, who came back to the box on May 29. Their first brood left on July 8. The male was more or less active in the territory and at box 6 until late in July but had no second brood. Probably he did not help much with the young out of the nest as he was at box 6 most of the time.

Territory No. 128.—Male, H18582, was active at box 25 on April 27, and in early May extended his territory to include box 11. However, on May 12 he had a return female, F45942, at box 25 and later allowed another male to supplant him

at box 11 (127). Their young left June 23. He probably helped to care for them, although he again became active at boxes 25 and 26 on June 29, and on July 14 had a female visit box 25 in the morning and box 26 in the afternoon without staying at either. The male remained around only a few days longer.

Territory No. 129.—Return male, C68910, was singing near the laundry and in front of the laboratory and active at boxes 21A and 49 during the latter half of April, first on April 14. On April 29 female, H18566, arrived and under the male's supervision inspected box 21A at 7:15 A.M., then box 21, and at 7:30 A.M. came to box 49 where she was more satisfied. She was trapped there on May 2 and deserted. When recaptured on June 13 (130), her right leg was noticed to have been broken at some time previous but was then healed. Did this occur on May 2? On May 1 the male drove off a male introduced into his territory from another estate. On May 2, when the female deserted, the male began some activity at boxes 51 and 53 as well as at box 49, but later gave up box 21 and 21A as another male took possession there (130). On May 6 a return female, probably F58248, was seen near but not at box 49. On May 20 she started her nest-lining in the box. Then the male ceased activity at boxes 51 and 53 and confined himself pretty largely here. By June 15, however, he was active as far east as the spring ponds. On June 24, while the male in territory No. 130 was busy with a female at box 92, male, C68910, was able to extend his territory into the maple grove. The young left box 49 on June 27. The male did not take much care of the young, as he was apparently the bird active at box 51 beginning June 27, and on June 30 he was at box 49. On July 1 he and an inspecting female were at box 53, but she did not stay. The male remained active at boxes 53 and 49 until the 5th, then was mostly inactive until the 9th when he returned to box 53. Female, H18820, came to that box on July 10 from an outlying estate where her young had flown about 12 days before. On the 15th the first egg was found to have been thrown out, possibly due to its being numbered. The nest was not deserted, and the young flew August 11. Possibly, but not certainly, this male was also the mate of the female that came to box 51 also on July 10 and laid 5 eggs before desertion. Perhaps the female here was the old one from box 49, as on July 12 she was captured at a banding station on the lawn east of the main house. She then was 3 grams over normal weight, as if laden with eggs.

Territory No. 130.—Return male, F45946, was probably the one singing near box 47 during the middle of April. Sparrows took over this box from April 28 to May 5, although the male continued more or less around. When the sparrow's nest was cleaned out for the third time on the latter day, the male wren began nest-building here more energetically and continued until May 9 or later. He took over box 21A about May 14, either driving out the male from territory 129 previously here or after that male had voluntarily relinquished it for his box 49. Male, F45946, had no further activity at box 47 which had become pretty well covered with vines. On May 17 female, H18566, 15 days after deserting box 49 (129), inspected box 21A and stayed. On June 26 the first brood flew. The male probably did not aid with the young after June 19, as he was at box 92. On June 20 a female came to that box. On June 26 the first egg was laid, but the wrens were continually in conflict with robins at a nest about 10 feet away. The robins got the better of the wrens, and on June 29 the female wren was gone, although the male stayed around for part of the day. On July 3, he was back at box 21A, and on the 4th a female, the same one as was at box 92(?), inspected that box but did not stay.

Territory No. 131.—An unknown male was at box 80 from April 29 to May 2 but was then absent until May 12. A female came May 16, but on the 29th her six eggs were destroyed, two being found on the ground with small punctures as if made by a wren. This male's territory probably extended beyond the limits of this area. He may have been the male heard in the ice pond woods on April 28 and 29.

Territory No. 132.—Male, H18570, was at box 74 on April 30 and at box 70 on May 12. A female had her nest-lining in box 70 and had deserted by May 20. During most of June there was only mouse activity here. By May 20 the male and

Fig. 19.—First breeding period, 1933

Fig. 20.—Second breeding period, 1933

perhaps the same female, F58493, return nestling, were at box 74. Their young were killed on June 24 by a small mammal. During the first week of June, the first week of incubation, the male's activity increased and he expanded his territory to the south. After the young were killed at box 74 he removed the lining on June 25 and 26, but was no longer active there. During the middle of July he may have had some activity at box 70 after the mouse had left and possibly also at box 72 in the ice pond woods, but no second brood was attempted.

Territory No. 133.—Male, H18588, was at box 72 in the ice pond woods on May 12 but later shifted to a natural cavity (Nest 169) and had a female with eggs on June 7. On June 15 the 5 young were found dead at 8:30 A.M. and the nest deserted. At 4:40 P.M. the male was captured at box 72A also in the ice pond woods. From June 16 to 19 this male was active at box 68 and perhaps even had a female starting to line a nest, but nothing came of it. By June 29 the male was on a neighboring estate across Mayfield Road where he had a second brood. The young there either left early or were killed, as one dead bird was found left in the nest on the 13th day after hatching.

Territory No. 134.—Return male, F45987, was at box 54A probably by May 12, and female, H18587, was there by May 20. On June 15 the young were killed and thrown out apparently by a killer wren (137) just before 8:30 A.M. I watched the unknown killer here from 8:30 to 10:00 A.M. and during this period he was chased three times by F45987. The killer was the more timid of the two and entirely quiet, while F45987 was pugnacious, chasing the killer, chasing another wren (female from box 49 (129)?), and visiting a nearby martin house. Later this pair of birds had the first egg of another set on June 23, and the young left on July 27.

Territory No. 135.—Male, L24102, was at box 43 by May 20, and at box 43A by May 29, possibly being forced out of box 43 previous to the 24th by the male in territory 136. Female, L24101, came to box 43A on June 2, and their young left July 7. There was no further activity here.

Territory No. 136.—Return male, F58648, was at box 40A on May 9 or earlier, and female, H18900, was here by May 16. This female had been brought in from an outlying estate and released at the laboratory on May 1. The young left on June 21, and there was no further activity at this box. During the incubation period this male wandered to box 34A by May 20, box 43 by May 24, box 92 by June 2, and box 79 by June 5. At box 43 female, H18584, arrived May 24, so that this male was polygynous. Probably he did not aid much in caring for the young in either of his two nests. Before 8:30 A.M. on June 15 the young in box 43 were found destroyed, probably by the killer male of territory 137. Male, F58648, had no further activity here. On June 29 he had his former female, H18900, at box 34A, 8 days after their first brood flew, and their second brood left August 5. The activity at box 37 on July 8 and 9 may have been by this bird and possibly also the July 3rd visit to box 92.

Territory No. 137.—Male, H18586, may have been a killer. The history of his activities, if they were all his, is here pieced together from scattered scraps of information and with some freedom of interpretation. Possibly there were two or more killers involved, but the facts can be explained by the activities of one bird alone. Possibly H18586 arrived in the region before May 5 but did not establish a territory. This was a peak year of wren abundance with 13 other first broods attempted and 12 territories established and with 3 pairs of bluebirds being present as well as sparrows and mice. Perhaps there was not room for another territory, and the activities of this bird may be explained by his attempt to make room. On May 5 the bluebird eggs in box 54 were destroyed, apparently by some bird. On May 29 the eggs at box 80 (131) were destroyed by a small bird. On June 1 the female bluebird was killed at box 68 and her eggs destroyed. From June 1 to 9 a new wren, probably this bird, was active at box 68 but then disappeared, apparently unable to establish a territory in competition with males in territories 129 and 132 and possibly 134 besides the male bluebird himself. On June 15 or late on
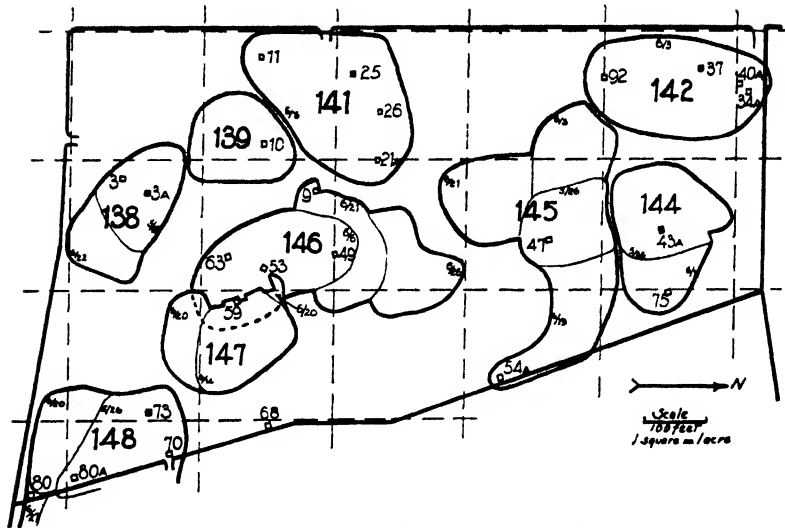
FIG. 21.—First breeding period, 1934
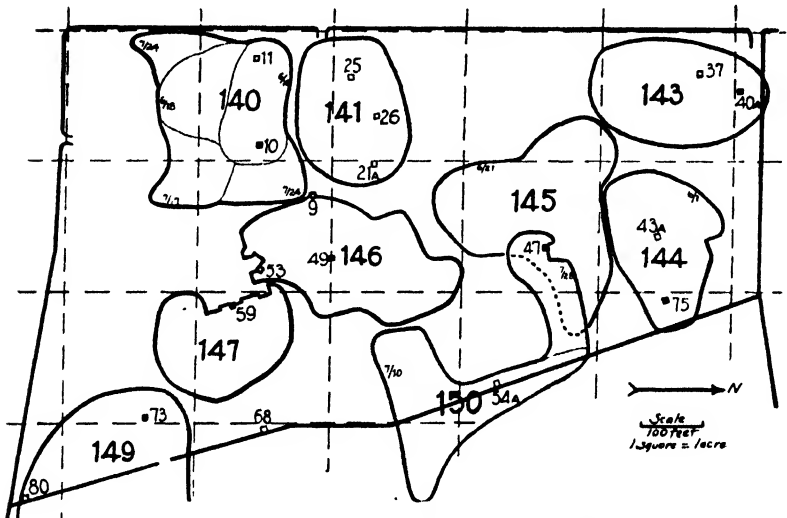
FIG. 22.—Second breeding period, 1934

June 14 he (?) ran rampant. The young at nest 169 (133) in the ice pond woods, at box 54A (136), and at box 43 (134) were destroyed before 8:30 A.M. I saw the intruding male at box 54A at 8:30 A.M. and even returned a couple of the young, still warm and alive, to the box, although they did not live. From 8:30 to 10:00 A.M. there was fighting between the two males here. At 11:00 A.M. I caught and banded this new male, who I believe was the killer, at box 79. He was one gram underweight. Was there a condition of hyperthyroidism in this bird? An unknown female came to him on June 18 but deserted her 5 eggs on the 26th, probably due to excessive heat at the box which was exposed to the sun. A male was singing here on July 6, but there is no other record of this bird.

1934 (Figs. 21, 22)

Territory No. 138.—Return male, L24102, was at box 3A by May 17 with female, L24948, and they raised their first brood by June 22. Probably it was he at box 3 by May 25 and who about June 18 got a female there to lay 3 eggs before she deserted on June 23. Did she desert because the male left her for his first brood? The male came back to box 3 on June 26 and cleaned house. However, he must have had a large part in care of the young, as on June 28 the female went to box 59 (147). On July 4, probably now free of the care of the young, he cleaned out box 3A but then disappeared.

Territory No. 139.—Male, L24956, was at box 10 by May 18 but apparently deserted when caught on June 16, not having obtained a mate. The limits of his territory can only be approximated.

Territory No. 140.—Male, L24933, came to boxes 10 and 11 in mid-June, and had female, L24987, at box 10 by June 22. Their young flew July 26. The male had meanwhile expanded his territory in various directions and included box 6 within it.

Territory No. 141.—Return male, H18600, was near box 25 by May 1, singing at box 21A by May 11 and at box 26 by May 16. He had return female, L24101, at box 25 on May 16, and their brood flew June 22. On June 16 the male lost out in competition for possession of box 11 with the male in territory No. 140. He must have had a large part in care of young out of nest, since the female had simultaneously started a second nesting at box 49 (146), 2 days before the young flew. The male later returned to clean house, then transferred chiefly to box 21A, where he had been slightly active during June. Perhaps on July 9 a female inspected this box but did not stay. The male remained active until about July 10.

Territory No. 142.—Return male, F58648, was at box 37 by May 4, at boxes 92 and 34A by the middle of the month, and at box 40A by June 1. However, on May 18 he had female, L24950, at box 37, and their brood flew June 27. He must have accompanied them for he disappeared.

Territory No. 143.—A male, 34-4277, appeared quietly on June 28 at box 40A and inspected the locality. He preferred box 37 and had a female half-heartedly interested in this box from June 29 until July 11. She may or may not have been L24950 who was still caring for her first brood out of this box (142), but anyway L24950 came to him in earnest at box 40A on July 12, fifteen days after her young had flown, and had a second brood leave August 15. The limits of his territory approximated those of territory No. 142.

Territory No. 144.—Return male, F45987, had female, L24955, at box 43A on May 18, and their young flew June 25. This male had added box 75 to his territory by June 1. On June 22 his female, L24955, came to him there although her first brood at box 43A did not fly for another 3 days. Her first egg was laid June 26. It is uncertain whether the female deserted box 43A when captured June 15; more probably it was a case with her of multiple nesting, with the male also interested in both nests. The male cleaned out box 43A June 28 to 30. Their second brood flew from box 75 on July 29.

Territory No. 145.—Box 47 was down and not replaced until May 18. A male was here by May 26 and at box 54A in early June but did not have a female inspecting until June 22 and 23. Female, 34-3509, whose young left a nest on a neighboring estate 10 days before, came to box 47 to stay June 27. The male was accidentally killed July 19 and the nest, being undefended, had the young killed on July 25, probably by the male from territory No. 150 who then became active here.

Territory No. 146.—Male, L24996, was more or less active at boxes 53, 59, and 63 during May but had largely shifted activities to box 49 by June 6. On June 11 and again on June 14 a female inspected box 49 but did not stay. On June 20, return female, L24101, came to this box, although her first egg was not laid until June 26. She was from box 25 (141) where her young did not fly until June 22, and she was noted caring for them on the 23rd. Perhaps this explains the long interval before her first egg was laid. Their young left box 49 on August 1.

Territory No. 147.—Male, L24954, was active at box 59 and visited box 63 during May, but during June he was mostly at box 59, displacing the male in territory No. 146. After the bluebirds deserted box 68 June 22 he attempted to add this box to his territory, but a red squirrel had taken it over by June 30. A female visited him at box 59 on June 15 but had left by the 22nd. Female, L24948, from territory No. 138 had been caught near the box on June 12 and came to him June 28, only 6 days after her first brood at box 3A had left, and they raised a second brood successfully.

Territory No. 148.—Male, L24946, was at box 73 by May 11, boxes 70 and 72 in the ice pond woods by May 18, box 80A by May 23. Female, L24944, was caught at a banding station in the old tennis court on May 19 and was at box 73, 2 or 3 days later. Her brood flew June 29. When the male was captured at this box June 14 he deserted, had some activity at box 80, then went across Mayfield Road and got female, 34-3502, there by June 25 and raised another brood.

Territory No. 149.—An unidentified male and female had a natural nest in the ice pond woods, and the male had probably been there since May 4 when he inspected box 72, but both deserted when the natural nest was transferred to a box on June 14. It is possible that the female was the one that inspected box 49 (146) the same day and on June 22 started a brood at box 10, being L24987 (140). The male is believed to have been at box 80 by June 27 and to have transferred to box 73 when female, L24944, came back about July 10, 11 days after her first brood had flown from here (148). The male had deserted by August 4 before he could be caught, but the brood left August 13 or 14. The territorial limits can only be approximated.

Territory No. 150.—Male, L24949, was at box 91 in the thick woods to the north of the barn by May 18 with female, L24951, and their young flew about June 24. This is not the best wren habitat. Five or more days before the young left, the male was at box 54A and came here for serious activity July 10-19 but did not get a mate. On July 25 the unprotected young at box 47, where that male had died (145), were found killed, probably by this male, L24949, as he then cleaned house and became active here. He disappeared near the end of the month.

1935 (Figs. 23, 24)

Territory No. 151.—Male, 34-86035, came to box 3 by May 13 along with a female. However, when she laid her third egg she deserted for some unknown reason. Female, 34-86036 (the same one?), was here by May 28. Two of their young left July 3 and probably the male cared for them. The rest left July 6. The male was more or less active around box 3 throughout July but did not remate. Sparrows occupied box 3A until their nest was removed on May 22, and during the middle of June a mouse was here, but from the end of June through July the male wren was active here.

Territory No. 152.—Male, 34-4239, came to boxes 10 and 11 by June 13 and stayed through July without getting a mate, although a female was with him at box 10 July 4-7 but left before she laid any eggs.

Territory No. 153.—Return male, L24956, came to boxes 25 and 21A by May 13. Return female, L24101, inspected box 21A on this date, was caught, and did not stay. She next showed up at box 25 by May 17, and her young left there June 25. During June the male was active in the maple grove, extending his territory even as far as box 92, although he did not prevent the male from territory 155 taking over that box on June 26. His female was caught on June 15 and deserted to appear at box 49 (160) two days later. The male was therefore forced to care for the young both before and after leaving the box. A new male had already become established at box 21A by June 13 (154), and on June 26 and 27, the two days after the young left box 25, there was intense competition in song for possession of the territory between the males from territories 152, 153, and 154, with the male of territory No. 154 winning out. By July 7 the young, then 12 days out of the nest, were independent and the male reappeared at box 92 with return female, 34-4201, whose young had left a box on a neighboring estate 11 days before. The male of territory No. 155 who was here for some days before was no longer active and did not offer much competition. The male became interested on July 25 in box 34 but deserted soon after August 1 when caught at box 92. The female brought off her brood successfully.

Territory No. 154.—Male, 34-86085, showed up at box 21A by June 13 with a female although she did not stay. Female, 34-86072, came to him on June 22, but her young were killed by a milk snake on July 22 and there was no further activity at this box. On June 25, the male of territory 153, who was caring for his young alone, had them leave the nest, and then for the next two days 34-86085 entered into a keen song and chasing competition against the males of territories 152 and 153 for the possession of box 25 and won out. By July 4 he obtained female, 34-4445, at box 25, whose young had left box 47 (159) nine days before. His activity at box 21A largely ceased except for occasional feeding of the young. By July 16 he added box 26 to his territory. On July 29 the female caught at box 25 deserted and on the 31st the male caught, deserted likewise, so the young had to be transferred to another box to keep them alive.

Territory No. 155.—Male, 34-86015, was at box 40A on May 13 and box 37 on May 17. On this latter date female, 34-86014, appeared and chose box 40A where she raised a brood by June 27. This male probably aided in the care of the young out of the box, as a new male came in immediately (156) and displaced him from his territory. On June 26 and 30 it was probably he who was at box 92, on the latter date with a female, perhaps the female from box 47 (159), but they did not stay.

Territory No. 156.—Male, 34-86088, and the male in territory 155 were competing for box 37 on June 26 and 27. Apparently 34-86088 won, and it was probably he who cleaned the lining from box 40A on June 28 and was at box 34A June 30. This male through most of July kept some activity at his various boxes but was mostly at box 34A. Female, 34-86014, whose young had flown from box 40A (155) fourteen days before, came to him at box 34A on July 11. On July 22 half of his mate's eggs were removed from the box by an unknown agent. Could it have been the female's former mate from territory No. 155 still around? On August 5 the male was caught and soon deserted. The female raised the young by August 19.

Territory No 157.—Return male, F45987, was at boxes 43, 43A, and 75 by May 13. Return female, L24955, came first to box 43A on May 17 but deserted on June 1 or 2 when her set of eggs was completed. I believe this desertion was due to her bringing in so many feathers from the nearby chicken yard that they overlay and interfered with her incubating the eggs. On June 3 she was down at box 75 and raised a brood there successfully by July 11, but only after I had removed the
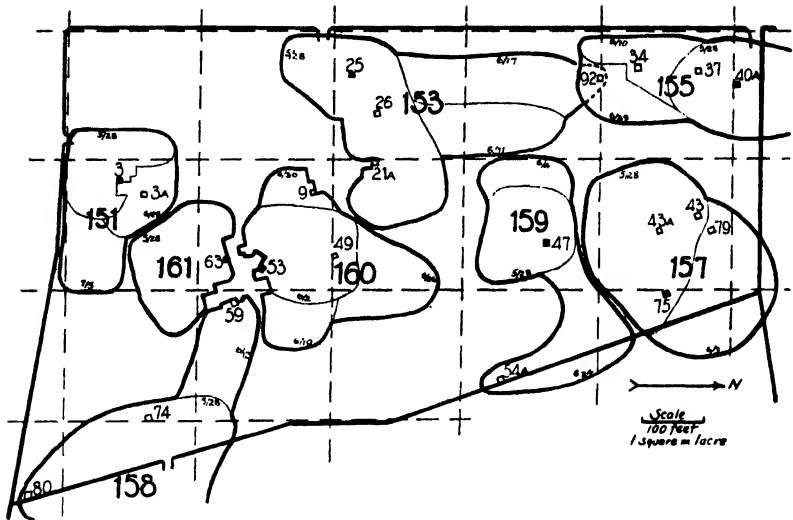
Fig. 23.—First breeding period, 1935
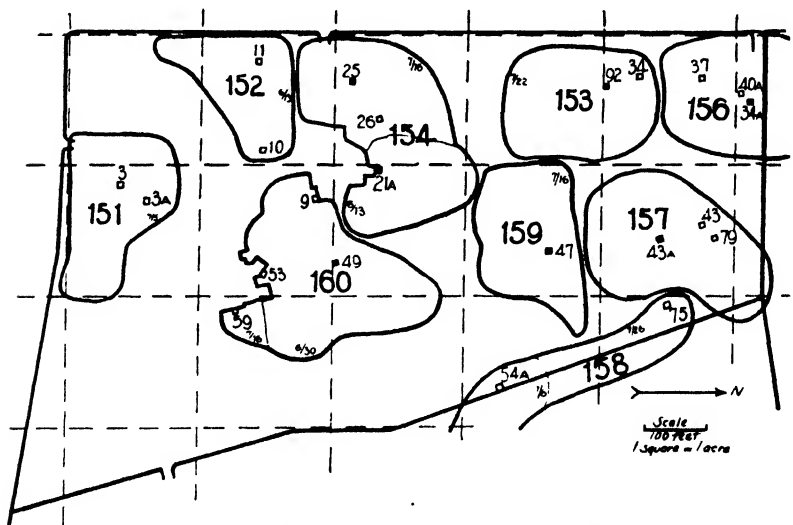
Fig. 24.—Second breeding period, 1935

excess feathers in her nest-lining as soon as the egg-set was complete. The male maintained possession of boxes 43 and 43A during June and had a female inspect box 43A on June 26. He probably did not aid very much in the care of his young out of box 75, as on July 15 he was active at box 79, and off and on during July at box 43A, and at box 43 July 18 to 24. On July 24 female, L24955, returned to him at box 43A, 13 days after her first brood had flown. She succeeded in raising a brood by August 28, not being bothered with excess feathers in her lining although there were plenty. The male deserted about August 5.

Territory No. 158.—This return male, L24949, was a restless one if our recognition of him through the season is correct. He was caught only once. By May 13 he had been at boxes 80 and 74. He was probably kept out of box 80 by wasps at first and later by mice. Mice also were troublesome for him at box 74. By May 17 he had replaced the mice in box 72 and was also very active at box 72A, both being boxes in the ice pond woods. On May 20 he restricted his activities largely to box 72 as a female came to him. However, on June 8 their eggs were gone and two adult mice with 4 or 5 young occupied the box. He again became active at box 80, and by June 12 he had added box 59 to his territory. By July 6 the male appeared at box 54A although still occasionally in the ice pond woods. He left here about July 16, and his final appearance was July 26 and 27 at box 75, encroaching on the territory of the male in territory No. 157.

Territory No. 159.—Male, 34-86013, was at box 47 by May 13 and with female, 34-4445, a return nestling, by May 17. On June 24 he was active at box 54A, but his young left box 47 successfully on June 25, the male aiding in their care. He was back at box 47 on July 1 or 2 and had a female on July 4 but not to stay for sure until July 6. Both adults left about August 1 when the eggs failed to hatch after 16 days of incubation.

Territory No. 160.—Return male, L24996, was at box 53 by May 13 and at box 49 by May 17. On May 24 a female came to box 49, but when on May 28 the nest was transferred to another box she deserted, probably going to box 53. However, she again deserted on June 15 or 16 as the eggs, replaced by dummies, were used in an experiment. On June 17 a female, probably L24101 who deserted box 25 (153) two days before, came to him at box 49. On June 24 she had laid 4 eggs, but around 7:00 P.M. they were all removed as if by another wren. Could it have been the male of territory 159 who on that date was searching for other boxes for activity and had been scouting down to box 54A? The female, however, spent the night in the box and laid a 5th egg the next day, a 6th egg June 26, then skipped 4 days to lay a 7th egg on June 30, an 8th on July 1, and a 9th on July 2, the last 3 eggs being recognized as from the same female by being very similar in markings and color to Nos. 5 and 6. No. 5 hatched late on July 10, No. 6 was found hatched early on the 12th, No. 7 early on the 14th, No. 8 early on the 15th, and No. 9 early in the afternoon of the same day. They all left the box July 28. The male was quite active in feeding the young, often more so than the female. He also visited boxes 53 and 9, the latter from June 30 to July 27. On July 2 a female inspected box 9 but did not stay. On July 25-27 he may have had a female with him inspecting box 59, but they did not stay.

Territory No. 161.—Return male, 34-4020, was at box 63 by May 17. On May 20 return female, L24944, came to box 63, and they raised their young by July 2, the male aiding in their care out of the nest. The female renested about 12 days later across Mayfield Road. The male did not renest.

1936 (Figs. 25, 26)

Territory No. 162.—Male, 35-13612, was in and out of box 3A by April 30 or May 2 and built a good stick nest soon after a sparrow's nest was removed on May 5. About May 15 he shifted his principal activity to box 3 as it was the choice of female, 35-13611, who had just arrived, even though it had a relatively poor stick nest. Their brood of young left June 21 under care of the female alone. Both

FIG. 25.—First breeding period, 1936

FIG. 26.—Second breeding period, 1936

adults were captured on June 21; the female persisted, but the male apparently deserted. On June 14 he was caught at box 59 where male, 35-13647 (163), had been listlessly active. Male, 35-13612, deserted this box 59 when captured and went down to the vicinity of box 73 where he had some activity carrying in spider nests and establishing a territory. However, he left the place entirely between June 21 and 24. His territory around box 3 is marked but his later wanderings are not shown.

Territory No. 163.—Male, 35-13647, was caught only on June 27 so he was not certainly identified through the season. However, a male was listlessly active at boxes 59, 73, and 74, especially box 59, all through the first breeding period. His lackadaisical defense of territory allowed male, 35-13612 (162), to progress through the area apparently unchallenged from June 12 to 21. However, a female, either 35-13635 or 35-13611, became established at box 59 on July 14. The eggs when due to hatch were replaced by dummies on August 1, but the hatched young birds and an unhatched egg were returned on August 2. On August 3 one adult was still around but not active at the box, and the young were dying through lack of care. This desertion of the young seems to be correlated with the poor development of reproductive vigor in the male.

Territory No. 164.—Male, 35-13634, was active at box 59 beginning April 30 and at box 53 beginning May 5. A female arrived at box 53 on May 14. About this time he gave up box 59, probably because he was much more interested in box 53, and another male (163) took possession there. For another box beside 53, he had by May 20 added box 49 to his territory. Due to my disturbance of the nest, the female deserted the eggs in box 53 on May 23 in the early afternoon. About 4:30 P.M. of the same day, two birds, probably this pair, were at box 49. However, female, 35-13635, did not become fully established here until May 27, so it was not certainly the same female throughout. On June 17 and 18 the first and second days after the young hatched, the male expanded his territory both to the east and west, perhaps to provide more room for finding food for young. On June 20 the female was captured and by the 26th she deserted, leaving the male to care for the young alone. The young left the box July 3. Presumably they remained under the care of the male, although he returned to boxes 49 and 52 for activity and song on July 6 and to box 49 again on the 10th and 13th, but no second breeding developed and the territory was not maintained.

Territory No. 165.—Bachelor return male, L24946, was first noted at box 11 May 25 and at box 10 May 27 but was possibly here earlier. He was unsuccessful in getting a female but kept adding new areas to his territory as the season progressed. On June 16 and 17 another male, presumably L24949, whose young at box 21A were just leaving (166), invaded the territory and became established at box 11. L24946 was either driven out or abandoned box 11 and became confined to box 10. Later he moved over to box 3A between June 27 and July 16, since the male there had left and was not defending that territory (162). He became quite inactive on this latter date, apparently discouraged by the lateness of the season in ever getting a mate.

Territory No. 166.—Return male, L24949, was active at box 21A and 26 before May 2 and at box 25 by May 4. Return female, L24101, arrived and selected box 21A by May 9. By May 20 he had extended his territory into the maple grove. Why did he not extend it southward toward the apple orchard as that seemingly is a better area and territory No. 165 was not yet established? On June 17 the young birds left the box and the male abandoned them at once. He wandered over to box 11 and succeeded in dispossessing bachelor male, L24946, of territory No. 165 who had been active there. While here, a new male (167) usurped his old territory around box 25 and separated him from the area around box 21A. On July 2 he succeeded in getting female, 35-13604, eight days after her young had left box 43A (170), and later expanded his territory to the southward. Their brood left on August 6.

Territory No. 167.—On June 23 male, 35-13670, became established at box 25 and two days later had a female here, 35-13671. Their brood left on July 31.

Territory No. 168.—Return male, 34-86105, was first active around box 34 about May 5 and visited this box or the vicinity until about June 17. He also knew of box 92 and his territory extended beyond here into the maple grove by May 9. About this time or soon after, a return female, 34-86014, arrived, and possibly guided by her he extended his territory to include box 40A where he and she raised a first brood which left the box on June 20. About June 12 he tired of his home duties and began to explore, visiting boxes 37 and 92, and possibly frightened by his capture at box 92 on June 16 wandered down to box 47 on June 29, a considerable distance away and only 4 days after the male there had completed his first breeding (169). On July 4 return female, L24951, 12 days after her first brood had flown from box 79 (171), came and by August 8 a second brood left the box.

Territory No. 169.—Return male, F45987, arrived at box 47 on May 2 or before; return female, L73248, came about May 19, and by June 25 their first brood had flown. While he was helping to care for the young, the male from territory 168 preempted his old box 47, so that when he was ready to nest again he was compelled to go elsewhere. He obtained female, 34-86014, who was the former mate of the male in territory 168, and together they started a nest at box 34A on July 2. She had been seen visiting box 92 on July 1 without a male around. It would seem she had completed the care of her first brood and was looking around for a suitable nest box even in localities not in any male's active territory. Possibly her visit to box 34A on July 2 was also when this territory was unoccupied, but that male, F45987, while he was roaming with his young, saw her there or in the vicinity and was induced to start a territory to fit the occasion. This nest and young were deserted on July 23. The male here was not caught and may have been a different bird from the one at box 37, but this is doubtful. About July 8, six days after the male, F45987, got his mate at box 34A, his former female from box 47, L73248, showed up at box 37 and they raised a second brood by August 14. Thus the male was polygynous. This is an interesting case of where two males switched their territories between the first and second breeding periods.

Territory No. 170.—Male, 35-13603, arrived at box 43A on April 28 or May 2 and during the rest of May expanded his territory to include boxes 75 and 54A. Possibly around May 10, a female came to box 75, after a sparrow nest was removed, and put in a lining but then left. Probably the same female, 35-13604, transferred to box 43A; by May 18 nesting had begun, and on June 24 the young left the box. The male was getting restless the last week before the young at box 43A flew, and from June 17 to July 16 he was intermittently active at box 54A. On June 22, return female, L24101, was secured at box 75, and the second brood left here on August 1.

Territory No. 171.—Male, 34-86997, arrived at box 79 by May 2, had return female, L24951, by the 9th, and their brood flew by June 22. This male had been active at box 43 off and on since May 5, and on June 21, a day before his young flew at box 79, he obtained female, 35-13653, at box 43, and their second brood flew July 29.

1937 (Figs. 27, 28)

Territory No. 172.—Male, 36-38805, was at box 3A by May 22. A sparrow nest at this box had not been removed until May 15. He was at box 3 and may have visited box 63 by June 8 and possibly box 52 by May 24. Sparrows occupied box 52 May 30-June 4. At box 3 there was a wasp nest during May. About May 29 female, 36-38803, came to box 3A, and their young left on July 4. The male had no great activity further at boxes 3 or 3A and probably had little to do in care of the young, as on July 6 he was back at box 63 and on July 13 he was active at box 52. A strange unbanded male had been inspecting box 52 a month previously on June 8-9. ·On July 9 female, 36-38397, whose young had left box 59 (183) twelve days before, came to box 63. Their second brood left August 11.

Territory No. 173.—Male, 36-38804, was at boxes 10 and 11 by May 5. From May 15 to 30 he had a female nest-building at box 11 but not laying any eggs. They then shifted to box 10 May 30 to 31, but she would not stay. On June 1 perhaps it was this male that, disturbed by the female's leaving, removed the eggs from boxes 25B and 47 (175, 182). The male remained active most of June at boxes 10 and 11 and later at box 7. At the latter box he had a female, June 23-24, but again she did not stay, and when this male was caught at box 10 on June 24 he left the place, going across Mayfield Road where he obtained a female and raised a brood.

Territory No. 174.—Male, 37-93969, was at box 7 by June 22 and later at box 11. His activities became concentrated at box 10 by July 6. Here female, 36-38803, came July 14, 10 days after her young had left box 3A (172), and they raised a brood by August 18.

Territory No. 175.—Male, 36-38374, came to box 25B by May 11 with a female nearby. A female started nesting here May 19, but on June 1, her 5 eggs were destroyed. This was the same day that 7 eggs were destroyed at box 47, apparently by a wren. Lining was removed from box 25B by June 5. A female (from 173?) came to him at box 25 on June 10, stayed a couple of days, but then left without laying eggs. He moved to box 21A about June 19 where female, 36-38865, came on June 25, and they raised a brood by July 29. During July and August he was somewhat active also at box 23.

Territory No. 176.—A return nestling of two years back, male, 34-86767, came late to box 25 about June 19 as the previous male there moved to box 21A (175). He had a female at box 25 on July 2-4, but she did not stay. The male then became very active at box 92 July 5-7 as a new female appeared there, but was back again at box 26 on July 8 along with a female, probably the same one visiting earlier at box 25. On July 14 she laid an egg here and deserted. The egg was poorly formed and abnormal. Could this female be the one attempting unsuccessfully to nest previously on several occasions at boxes 10, 11, 7 (173), and 25 (175, 176)? There is no further record of her. On July 16 the egg was gone from box 26, and in a day or two the male had female, 37-93972, at box 25. Their young left on August 22.

Territory No. 177.—Return male, F45987, was at box 34, which had been replaced May 15, by May 19 along with female, 36-38389, and had added box 92 to his territory by May 31. When caught June 16 his leg was found broken and it was amputated. The male may have persisted around until the end of the month but was not very active. His undefended territory received visits from the male of territory 178, but the female raised her brood by June 26.

Territory No. 178.—Return male, L24949, was at box 37 by May 5, but a robin built on top of the box, so that the male did not become really active here until early June when the robin's nesting was over. He may have destroyed her eggs. By May 10 he had female, 36-38381, at box 40A, and their brood flew June 19. The male did not aid much in their feeding, and on June 10 when the female was scolding at the box a strange male showed up for a moment, then disappeared. He may have been a non-breeder momentarily interested. After the young left, male, L24949, removed the lining from the box on June 21 and then shifted to box 37. A female visited him there June 23. For the next two or three evenings, but not much during the day, a female, probably 36-38381, repeatedly visited him at the box but not to start nesting until June 26, only 7 days after her young had left box 40A. After getting his former female re-established at box 37 he became active at box 34 on July 3, since the male there was one-legged and mostly inactive (177). On July 5 there was competition in song for possession of boxes 34 and 92 and surrounding territory between this male, the old one-legged bird from territory 177, the male from territory 176, and a new one. L24949 had won out at box 34 by the next day, and the new male at box 92 (179). On July 7 the female, who may have incited the rivalry on the 5th, appeared early in the morning at box 92 and then shifted to box
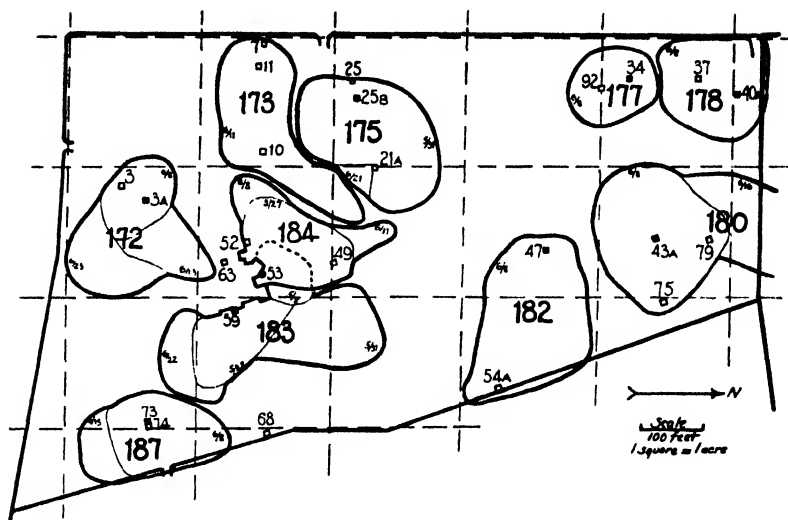
FIG. 27.—First breeding period, 1937
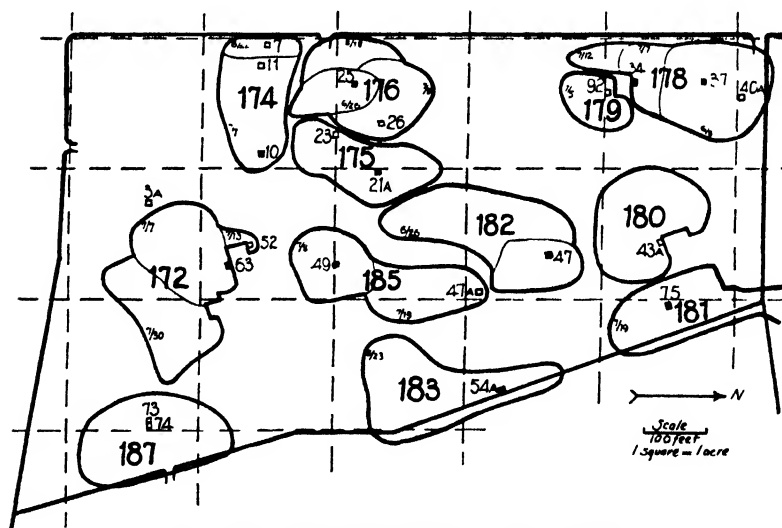
FIG. 28.—Second breeding period, 1937

34. She was 36-38389, the female formerly at box 34 (177), whose young had left 11 days before. She started a second brood that left August 12. This male then was polygynous but did not help the box 34 female much, although he would come around when she scolded. By August 1 the box 37 female had deserted for unknown cause and he had to care for the young there alone. The young flew August 4.

Territory No. 179.—An unidentified male succeeded in establishing a territory around box 92 beginning July 5, after severe competition with the males of territories 176, 177, and 178. A female inspected box 92 on July 7 but then moved over to box 34 in territory 178. The male remained around during July but did not find a mate. His territory is only approximately indicated.

Territory No. 180.—Return male, 35-13603, was at boxes 43A and 79 by May 5. Return female, L24951, was at box 79 on May 11 but left after being caught. She reappeared at box 43A on May 17, and their brood left June 25. The male had added box 75 to his territory by late May and was more or less active here until early July. Through July he was mostly around box 43A as a new male occupied box 75. About July 26 a female came to box 43A but laid only 2 eggs and deserted before August 8.

Territory No. 181.—An unbanded male took possession of box 75 by July 19 and had female, 37-93983, by July 24. The male had deserted by August 13, and when the female was caught on this date, she also deserted, leaving the young to starve to death. His territory is only approximately indicated.

Territory No. 182.—Male, 36-38856, arrived at box 47 by May 5 and had obtained a female by May 15, but their eggs were destroyed June 1 by a killer wren (173). The male removed the old nest-lining by June 3 and then became active at box 54A, June 8-13, where a sparrow's nest had been recently removed. By June 21 he was back at box 47 with female, 36-38040, a return nestling, and raised a brood by July 27.

Territory No. 183.—Male, 36-38378, was at box 53 by May 5 but when caught there on May 18 stayed away. He succeeded in getting female, 36-38397, at box 59 May 22. Their young flew June 27. The male apparently left box 59 before the young flew as he appeared at box 54A on June 23. Why did he go way off here? Did the male in territory 184 disturb him? At box 54A he had female, 35-13914, on July 7, whose first brood had left or been destroyed on an outlying estate but a few days before. They raised their brood by August 11.

Territory No. 184.—Return male, 34-86015, was at box 49 by May 15 and at box 53 by May 27, after the male in territory 183 had been caught there and deserted. On June 2 he obtained female, 36-38811, at box 53, and thereafter was at box 49 only infrequently, losing it entirely to a new male that came in on July 8 (185). His young at box 53 flew July 9. He disappeared then as the new male offered strong competition on July 8 and drove him out. His resistance was probably weakened by his care of young.

Territory No. 185.—Male, 35-13912, had a first brood to leave a box on a neighboring estate near the end of June and for some reason transferred over here to box 49 on July 8. He wrested this box from the male of territory 184 who was then busy caring for his young which were on the point of leaving the box. He obtained female, 36-38390, also on July 8, ten days after her young had left box 73 (187), and they raised their young to fly by August 12. He had some activity at box 47A by July 19.

Territory No. 186.—Male, 35-13700, was at box 72A in the ice pond woods with female, 36-38388, by May 14, and their young flew June 22. He was also at box 72 near the end of May but was not active. Mice came in there June 21-30. The male went across Mayfield Road and had another female by June 13, and this female raised a brood. Female, 36-38388, also went off the estate and was remated about
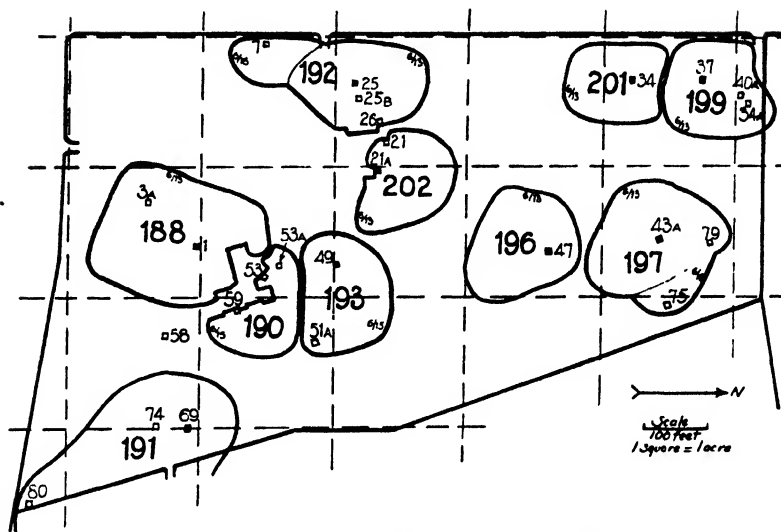
Fig. 29.—First breeding period, 1938
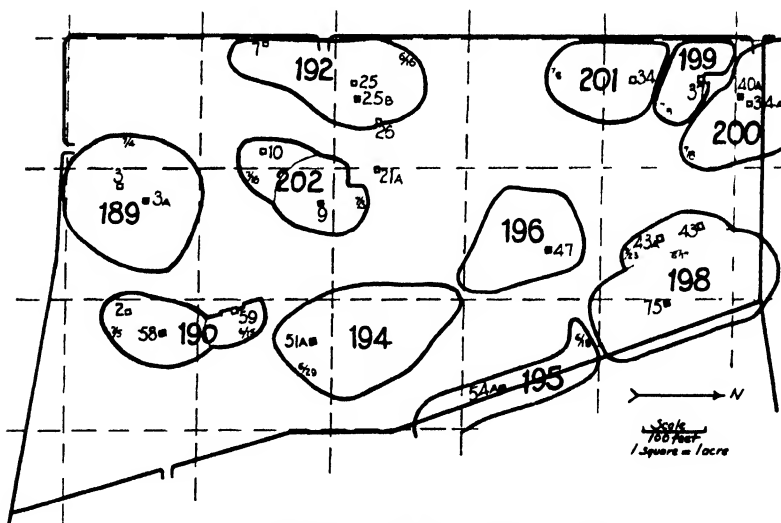
Fig. 30.—Second breeding period, 1938

June 23. It is uncertain which adult cared for the brood of young from box 72A or whether it was destroyed. The territory is not shown.

Territory No. 187.—Male, 36-38375, was at box 74 by May 11 and transferred to box 73 on May 17 when female, 36-38390, chose this box. Their brood left June 28. The male had expanded his territory in the direction of box 68 by June 1, although not active at the box itself. After the young left box 73 he was back at box 74 by July 6. He remained around until about July 17, and it may have been he with a female that was around the box in the early morning of August 4.

1938 (Figs. 29, 30)

Territory No. 188.—Male, 38-1640, and female, 38-1610, came to boxes 1 and 3A by May 11 and raised a first brood at box 1 by June 20. After the young left, the male was active on June 22 and 23 at box 3A, but that is the last record of him.

Territory No. 189.—Male, 36-38429, came to box 3 by June 27 and on July 4 went to box 3A. He had little trouble establishing a territory around these boxes as the male in territory 188 had left. Female, 36-38428, arrived at box 3A on July 6, and they raised a brood.

Territory No. 190.—A male, probably 38-1655 throughout, started activities and nest-building at box 58 May 11-18, but was displaced here by bluebirds who successfully raised a brood using the wren's nest instead of one of their own. The male then became active at box 53, May 27 to June 17, where a female visited him on June 13 but did not stay, at box 53A on June 8-15, and at box 59 June 8-28. The bluebird's brood left box 58 on June 28, and the male wren returned here the next day. On June 30, the following day, female, 38-1610, whose first brood left box 1 (188) 10 days before, arrived, and they raised a brood that left on August 4. On July 5-7 while the female was laying eggs, the male had some activity also at box 2.

Territory No. 191.—Wren activity had already started at box 69 by May 4 when there was one egg present. By May 11 house sparrows had come in, destroyed the wren's nest, and started one of their own which we removed. This incident caused male, 35-13700, return adult, to scatter his activities to boxes 74 and 80. On May 28 he was back at box 69 with female, 38-1662, and they raised a first brood which left on July 5. Possibly when they were through caring for the young it was too late in the season to start a second brood.

Territory No. 192.—Male wren, 38-1609, had started at box 25 by May 4 and had female, 38-1608, by the 11th. Their first brood was out of the box on June 17. He may have helped to care for the young but at the same time was more or less active at boxes 26 and 25B, and had his former female restarted for a second brood at box 25B by about July 4. While actively remating and preparing for this second nesting, he probably in his excitement went to box 7 on July 4 or 5 and destroyed a new set of bluebird eggs. The wren's nesting was unsuccessfully terminated on July 25 because of interference.

Territory No. 193.—Male, 38-1641, started at box 49 about May 11, female, 38-1642, was here by May 18, and their first brood left the box on June 25. At box 51A bluebirds started to nest May 4-11 but were destroyed by sparrows, and the sparrows' nesting was stopped by me May 18-21. The male from box 49 was occasionally here, June 3-22, but was not seen there later. On June 27 and 28 he removed the used nest-lining from box 49 but had no further nesting activity. He probably was occupied with caring for his young out of the box, as his female, only 4 days after the young left, mated with the male in territory 194.

Territory No. 194.—Return male, 37-93876, appeared at box 51A about June 29, and either the male in territory 193 had gone to care for his young or he easily succumbed, as the new bird quickly carved out a territory of his own. He obtained female, 38-1642, only 4 days after her young had left box 49 (193), and their brood left the box on August 3.

Territory No. 195.—From May 4 to June 13 sparrows held box 54A but then the female sparrow and nest was destroyed by me. On June 18, male wren, 36-38427, appeared. From June 24 to July 2 the male successfully withstood persistent competition for the box with a male bluebird, and on the latter date female wren, 36-38426, started here, and they raised a brood that left on August 4.

Territory No. 196.—On May 4, male wren, 36-38856, came to box 47 and on May 11 female, 36-38040, was also here, both birds having been mated together for a brood last year at this same box. The young left on June 16, the lining was removed June 21-22, and a second brood started June 29, but it did not turn out successfully.

Territory No. 197.—An old male from 1935, 1936, and 1937, No. 34-86015, started at box 43A on May 4, got a female, 38-1607, by May 11, and raised a brood by June 17. He was also somewhat active at box 79 from May 4 to 18 and at box 75 from May 27 to June 8 after a sparrow's nest was removed. He disappeared at the end of the first breeding period.

Territory No. 198.—From June 14 on, male, 38-1684, came to box 75, and while the male of territory 197 was partially occupied with the young from box 43A, successfully wrested away this box and territory. On June 24 he even secured female, 38-1607, formerly of territory 197 and whose first brood left 7 days before. They raised a second brood to leave on July 30. During July and early August male, 38-1684, expanded his territory to include boxes 43A and 43, and on August 4 a female wren visited him at box 43A.

Territory No. 199.—Male, 38-1654, was active at box 37 on May 4, and a last year's female, 36-38389, came here on May 19. They raised a first brood to leave on June 24. During May, but not during June, this male was also somewhat active at boxes 40A and 34A. After the young left box 37, there was little activity in the territory until July 5 when male wren, 34-86997 (200), an old bird from 1936, came in and carved out a territory around boxes 34A and 40A. The competition in singing was intense, at least from July 8 on, between this new bird, 38-1654, and also the one in territory 201. No. 38-1654 pulled out the old lining in box 37 and was more or less active until August 2 without success in getting a new mate.

Territory No. 200.—Male, 34-86997, came to box 40A in territory 199 on July 5 and successfully carved out a territory of his own. He did not meet much competition until July 8, the day after he obtained female, 36-38389, of box 37 (199) who had young out of the box 14 days before, as the male was busy caring for his young. Their brood left on August 11.

Territory No. 201.—An old male wren, 35-13603, from 1936 and 1937 came to box 34 on May 4. An old female from 1937, 36-38811, came here on May 11 and had a first brood leave the box on June 17. On June 27 the male was back, tearing out the old nest-lining. On the 28th his former female returned and on July 8 had laid 4 eggs. On July 9 these eggs were gone. This was the period beginning on July 8 when the arrival of the new male at box 40A caused intense feeling and competition between the males in territories 199, 200, and 201. Either in his excitement male, 35-13603, destroyed his own mate's eggs or he allowed one of the other of the two males to come in and do so. Probably the first is true, as the other males appeared confined to the vicinity of their own boxes. In that case, it is an interesting setback to an earlier phase of the nesting behavior pattern. The female left and went to box 9 in territory 202, while the male remained partially active in his territory until at least July 26.

Territory No. 202.—Male wren, probably 38-1681 throughout, started at box 21, May 11, and showed some activity, beginning May 18, at box 21A. About May 22, female, 38-1611, came to box 21A, and by July 11 their brood was raised. From May 18 to June 12 there was some activity at box 9, but it is uncertain whether of this male or the one from territory 193. However, on July 2 or 3 male, 38-1681, deserted the female with young at box 21A and became active at box 9. He had a

good male nest. On July 3 he was visited by a female wren who did not stay. This may have been female, 36-38811, who had started to nest for the second time at box 34 in territory 201, but was apparently away from there for a couple of days just about this time. Anyway female, 36-38811, returned to box 34 and laid 4 eggs by June 8 when some territory strife set in and her eggs were destroyed. Due to lay her 5th egg on July 9 she returned to do so in the male's nest at box 9, even though this nest was without lining and presumably this male had not fertilized the eggs (or had he?). This egg was gone on July 10, however, probably destroyed in the process of the female's carrying of nest-lining into the box. The identity of this female was recognized from the sequence in egg weights and colors. On July 13 to 15 she laid 3 eggs, this time probably fertilized by male, 38-1681, but thereupon she deserted for unknown reasons. The male wren transferred his activity to box 10 until caught there on July 19, whereafter he returned to box 9 until late in the month.

1939 (Figs. 31, 32)

Territory No. 203.—Male, 36-38466, arrived June 21 at box 1. Sparrows had nested here previous to June 10, and the male was mostly kept away from box 3A by sparrows nesting nearby. On June 23 the male was observed silently to inspect box 9 outside his territorial limits, then fly down to box 49 where he was chased back to box 1 by the male in territory 208 who had a first brood there. Female, 36-38465, was first observed at box 1 on June 27. Their young left August 5. The maps of this territory show how additional areas are added with time to an originally small territory. After the young left box 49 (208), the male added this area to his territory, and on July 26-28 successfully defended it against the male of that territory who returned from caring for his young.

Territory No. 204.—Male, 36-38461, was at box 10 by June 10 and female, 38-1607, a return from the year before, came about June 21. Their territory extended to the southwest in the only free area. Their young left July 27.

Territory No. 205.—Male, 36-38427, a return from last year, came to box 11 between June 10 and 14, and since the surrounding area was largely occupied had to squeeze in his territory along the western fringe. Female, 36-38462, came June 21, and their brood left July 29.

Territory No. 206.—Male, 36-38456, and female, 36-38452, started nesting at box 23 about May 21. Their young left June 27. The male was at box 21A before June 10 but not seriously until the 25th. He probably did not care for his young out of box 23 after one or two days, as a new male appeared who by persistent singing established territory 207. Male, 36-38456, defended his possessions to the extent of getting established at box 21A by June 30. On July 4 he went down to box 49 investigating, but was chased back. On July 6, an unbanded female came, for the next 2-3 days inserted lining into box 21A, but did not stay. By at least July 11, female, 36-38459, was here, 6 days after her young had left box 47 (211) being cared for by that male. Their brood left August 12.

Territory No. 207.—Male, 36-38467, appeared first on June 29 at box 23 where he was chased away by the male in territory 206. However, he returned and by vigorous singing established himself a territory centering at box 25. On July 8 female, 36-38452, whose first brood at box 23 (206) left 11 days before, came to him instead of to her former mate already mated at box 21A, and their brood left August 11.

Territory No. 208.—Male, 36-38429, a return from last year, was with female, 36-38426, also a return, at box 49 about June 4 and they raised a brood by July 10. He apparently flirted with another female at the same time as she laid one egg in box 53 by June 10 and then deserted. On the 16th, she again appeared, starting a new lining in box 53A but not proceeding further with it. On the 16th the male competed in song with the male in territory 210 on the front lawn and later with the male from territory 203 at box 59 but gave up box 59 to that male.
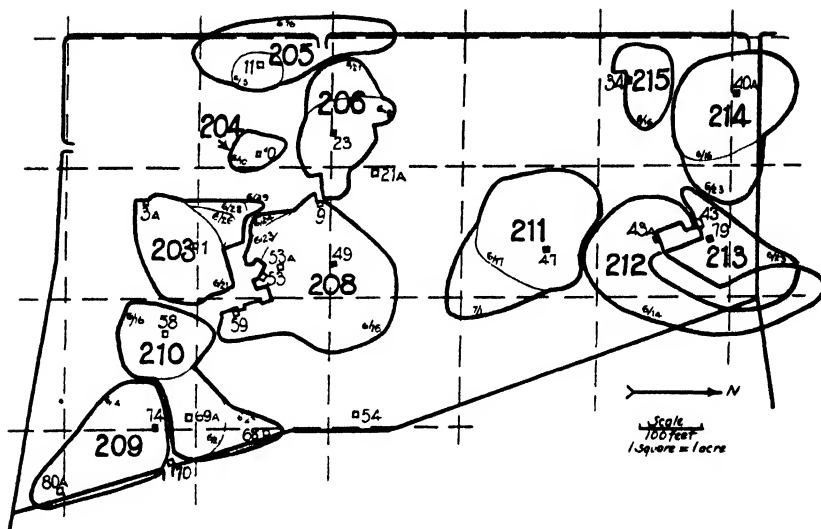
FIG. 31.—First breeding period, 1939
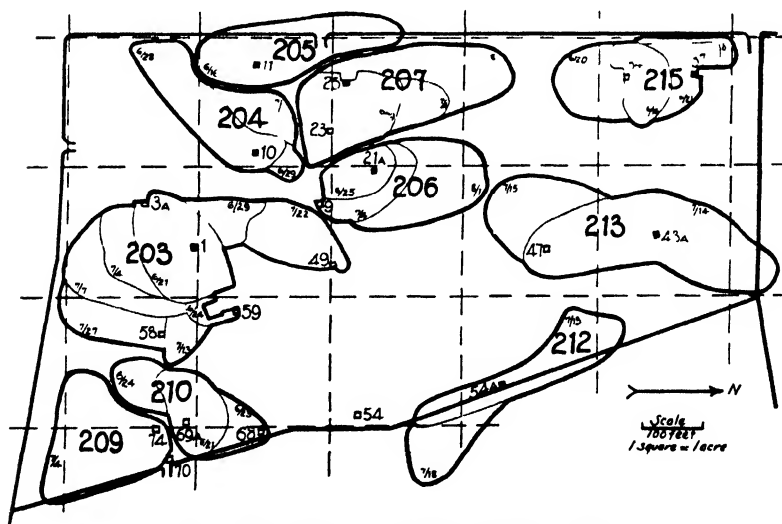
FIG. 32.—Second breeding period, 1939

On July 4 he chased away the male of territory 206 from his box 49. The female at this time was going a considerable way to the east outside of his territory for food for young. On July 10 the young left with the male caring for part of them. July 26-28 it was probably he who returned to box 49 but was driven away by the male of territory 203 who had expanded his territory in this direction. Then the male disappeared.

Territory No. 209.—Male, 36-38454, was active at boxes 74 and 80A during May. About May 17 female, 36-38453, came to box 74, and their brood flew June 22. Queer happenings occurred around this box. On June 13, the male was observed to chase up into the rose garden two other wrens, one a red-banded male, the other unbanded and probably from territory 210. The next day and again on June 18 he was observed to chase away a wren, probably in both instances the unbanded male from territory 210. Almost three weeks later, on July 4, a red-banded quiet male, appeared at box 74, possibly with a female, and inspected the box. No. 36-38454 acted toward it in an excited manner as if it were a female. Then on July 8, these two red-banded males, the box 74 male singing excitedly, the strange male quiet, inspected boxes 68, 70, 74, and 54 with boxes 68, 70, and 54 being outside of 36-38454's territory. There was no chasing and 36-38454 acted toward the other as if it were a female. Could this have been a male looking for a place or an opportunity to begin establishing a territory? Perhaps until he finds a place that is suitable, a male does not advertise his scouting expenditions by song, and other males react toward him as a female? Could some of these other inspections of boxes generally considered to be by females sometimes be actually males looking for territories? This box 74 male had cleaned house July 3 and was occasionally active around his boxes, but since his female deserted about June 21 he had to divide his time with caring for young. By August 3 he had ceased activity in the territory.

Territory No. 210.—An unidentified unbanded male was at box 58 by June 10 or soon after. He was bothered by bluebirds at a nearby box who had formerly nested at box 58. He may have been around box 74 from June 13 to 18 (209). He was at this time also becoming active at box 69A. Sparrows were starting a set of eggs here. I removed them on June 19, and the sparrows started to rebuild. On the 20th the wren was observed rearranging this sparrow nesting material to his own needs and on the following day was adding sticks. On June 21 the female at box 74 had lost interest in feeding the young there and came around boxes 58 and 69A apparently interested in these boxes and this male. At box 69A she was driven away by sparrows, especially by the female sparrow, who had started to build again. The male wren was obviously disturbed by sparrows building here but did not chase them. He once went into the box when the sparrows were away and removed a feather. The male at box 74 was busy feeding his young and did not defend his territory against the box 69A male very vigorously, although this male was enticing his female away. On June 23 the sparrows appeared to have won out at box 69A, since they had 2 eggs and the male wren had shifted activity to box 68. On June 24 this male wren recaptured box 69A and threw out the sparrow eggs, and the sparrow showed no inclination for further competition for its possession. The box 74 female visited box 69A, and the male got excited each time but he did not maintain his excitement at a high pitch for very long. The female seemed not able to respond sufficiently to start nesting. On July 25 the pair were found in an orchard east of the old tennis court. On my squeaking the male got excited and attempted copulation with the female but unsuccessfully. The female seemed not to have sufficient sexual vigor to accept copulation. By July 29 the male was still seen occasionally near boxes 69A and sometimes near box 74 but was quiet and about ready to give up possession of his territory.

Territory No. 211.—Male, 36-38458, had female, 36-38459, at box 47 by May 30. The young left July 5 with the male aiding in their care and then disappearing. With him gone the male from territory 213 took possession about July 6.

Territory No. 212.—Male, 36-38457, had female, 36-38455, at box 43A by May 19. On June 17 she was caught, after which she was not very attentive to young. She may have brooded them at night as they were only 5-6 days old, but she did not feed them during the day. She remained in the bushes near the box where she was occasionally seen during the daytime. Finally by June 26 she began to regain her former behavior and to take part in their care. The young flew June 28, the male aiding in caring for them. While wandering with the young, the male found box 54A and transferred to it by July 8. He was probably with a female at that time as she, 36-38455, laid her first egg on July 11. She was his old mate from box 43A where her young had flown June 28, 10 days at least before she came here. Transference to box 54A was aided by the fact that the male in territory 213 took over their territory around box 43A on July 2 while the male was busy with the young and did not defend it. Swarms of sparrows persisted around box 54A and the male remained close to it for defense. It is doubtful if he fed the young from box 43A much after July 8. On July 12 the eggs from box 54A were gone, probably destroyed by sparrows, but the female laid 2 more. By August 2 the male had deserted, but the young came off successfully on August 13.

Territory No. 213.—Male, 36-38856, a return, had female, 36-38040, also a return, at box 79 by May 11, and their young left June 21 with the male aiding in their care. There appeared to be some tolerated overlapping or neutral area between territories 212 and 213 in the barnyard for some days. By June 10 he had been at box 43. On July 1 he cleaned out box 79, and since the male in territory 212 was gone with young he also cleaned out box 43A on July 2 and got the female, 36-38040, his former mate, about July 4, 13 days after their first brood flew. Their second brood left August 6. The male took possession of box 47 about July 6.

Territory No. 214.—An unidentified return male had a female at box 40A by May 27, but on June 19 the newly hatched young were gone, and the female deserted. The male was no longer active at the box, although on June 24 a male, probably he, challenged the male in territory 213 for the attentions of a female near box 43. The other male chased the female into the woods, and there is no further note on this bird. His territory was partially taken over by the male in territory 215.

Territory No. 215.—Male, 36-38464, was at box 34 with a female in early June. On June 20 the female deserted her eggs for unknown cause—this about the same time as another female deserted box 40A (214). For the next couple days the male cleaned house, sang near the box, and then transferred to box 37. A female may have been near there June 25 but not to stay until the 27th. She was No. 36-38463, possibly the one from either box 40A (214) or box 34. Their young left August 3.

IX. HISTORY OF INDIVIDUAL BIRDS

A CONDENSED SUMMARY of the territories and boxes occupied and the mates secured by ninety-eight birds is presented in table form. Only birds are included which were present two or more years on Hillcrest. When the bird hatched on Hillcrest its first record in the table is indicated as that of a "nestling," and the box number given is that in which it hatched; likewise the band numbers of its "father" and its "mother" are included. The nestling records of these birds are put in the proper columns for the breeding period in which they hatched. Unmated birds are designated as "bachelors." For further account of these birds reference should be made to the case histories in the preceding section.

TABLE 5.—LIFE RECORD OF INDIVIDUAL BIRDS

Band Number and Sex	Year	First Breeding Period			Second Breeding Period		
		Territory	Box	Mate	Territory	Box	Mate
6882 Female	1923	36	51	26600	36	59	26600
	1924	46	51	A20	46	68	A20
6891 Female	1923	34	40	26546	33	37	6888
	1924						
	1925	56	47	57759	57	47	31852
6892 Female	1923	37	59	26601			
	1924						
	1925	49	3	58023			
6899 Male	1923	27	3	6881	27	63A	57798
	1924	47	68	?			
		47	59	57799			
	1925	53	68	153	(Male died)		
21212 Female	1921	1	3	45963	10	63A	45335
	1922	19	37	26512	19	37	26512?
	1923	29	30	22995			
21231 Male	1921	5	37	21211	5	37	21211
	1922	17	30	45303			
21264 Male	1921	8	53	21234	8	49	21234
	1922	24	53	22987	24	53	22988
22995 Male	1922	12	6 25	Bachelor			
	1923	29	30	21212			
		29	25	6885			
26523 Male	1922	13	6, 3	Bachelor			
	1923						
	1924						
	1925	55	51	26551	55	9	26551
26546 Male	1922	20	47	22988			
	1923	34	40	6891			
	1924	44	43A	A10	44	75	A10
26551 Female	1922	20	47	Nestling			
		(Father 26546, Mother 22988)					
	1923				32	25	57783
	1924	39	6	58023	39	6	58023
	1925	55	51	26523	55	9	26523
26600 Male	1922				14	6	26595
	1923	36	51	6882	36	59	6882
26601 Male	1922				21	47	22989
	1923	37	59	6892			
27739 Female?	1915		9	27740		49	?
	1916		49	38491			
44008 Sex?	1917		51	44009			
	1918		51	44100			
	1919		9	44100			
44100 Sex?	1918		51	44008			
	1919		9	44008			
44526 Sex?	1918		40	44525			
	1919		40	, ?			
45206 Male	1918					47	45205
	1919		26	45311			
45303 Female	1919		25	45302		53	45349
	1920		25	45342		25	45342
	1921	2	25	45342	1	6	45963
	1922	17	30	21231	16	25	26638
45325 Female	1919		3	Nestling			
		(Father 45324, Mother 45322)					
	1920					59, 53	45968
45335 Male	1919		63	45334			Bachelor
	1920		63	45988		49	45955
	1921	10	63	21206	10	63A	21212
	1922	11	3	?	(Male killed)		

TABLE 5.—LIFE RECORD OF INDIVIDUAL BIRDS (*Continued*)

Band Number and Sex	Year	First Breeding Period			Second Breeding Period		
		Territory	Box	Mate	Territory	Box	Mate
45342 Male..............	1919	....	25	Bachelor	....	....	.....
	1920	....	25	45303	....	25	45303
	1921	2	25	45303	2	3	21206
	1922	23	52	22989	23	63A	22989
45349 Male..............	1919	....	....	.....	....	53	45303
	1920	....	....	.....	....	47	46006
45963 Male..............	1920	....	49	Nestling	....	....	.....
		(Father 45335, Mother 45955)					
	1921	1	3	21212	1	6	45303
45968 Male..............	1920	....	....	.....	....	59, 53	45325
	1921	6	47, 75	46006	6	47	21294
46006 Female............	1920	....	....	.....	....	47	45349
	1921	6	47, 75	45968	9	68	48775
48775 Male..............	1921	9	59	21213	9	68	46006
	1922	25	59	26502	....	....	.....
48785 Male..............	1921	2	25	Nestling	....	....	.....
		(Father 45342, Mother 45303)					
	1922	15	23	26520	15	26	22987
	1923	35	47	6884	35	47	6885
	1924	41	25	58024	41	23	A87
57759 Male..............	1923	....	....	.....	38	53	57799
	1924	45	47	A27	45	....	.....
	1925	56	43	A167	56	43A	A167
		56	47	6891	....	....	.....
	1926	58	25	(Died)	58	11	38446
57799 Female............	1923	....	....	.....	38	53	57759
	1924	47	59	6899	48	63	A15
58023 Male..............	1924	39	3	A28	....	....	.....
		39	6	26551	39	6	26551
	1925	49	3	6892	49	6	31917
63810 Female............	1926	59	49	A34236	59	51	A34236
	1927	64	59	A34236	....	....	.....
664708 Female..........	1928	80	37	?	81	75	?
	1929	82	37	B97101	....	....	.....
664751 Female..........	1928	75	6	A94249	75	10	B94249
	1929	91	63	A93433	....	....	.....
A20 Male................	1924	46	51	6882	46	68	6882
	1925	54	59	A183	54	63	A183
A50 Male................	1924	....	....	.....	43	37	Bachelor
	1925	....	....	.....	....	....	.....
	1926	Outfield	A5	63774	....	....	.....
A61 Male................	1924	45	47	Nestling	....	....	.....
		(Father 57759, Mother A27)					
	1925	52	....	Bachelor	....	....	.....
A34236 Male.............	1926	59	49	63810	59	9	?
		....	....	.....	59	69	?
		....	....	.....	59	51	63810
	1927	64	59	63810	64	....	?
A38398 Male.............	1926	Outfield	A71	Nestling	....	....	.....
		(Father 38386, Mother 63811)					
	1927	63	6	A93420	....	....	.....
	1928	78	....	Bachelor	78	51	B45348
	1929	89	51	B45348	....	....	.....
	1930	98	51	B45348	98	50, 51	.....
A93433 Male.............	1927	61	80	A94233	....	....	.....
	1928	73	74	B45349	73	70	B45321?
	1929	91	63	664751	91	59	?
	1930	102	74	C68257?	102	70	.....

TABLE 5.—LIFE RECORD OF INDIVIDUAL BIRDS (*Continued*)

Band Number and Sex	Year	First Breeding Period			Second Breeding Period		
		Territory	Box	Mate	Territory	Box	Mate
A93526 Female	1927	Outfield	A38	A93697			
	1928	76	25	664601	(Female killed)		
A93573 Male	1927	Outfield	A15	Nestling			
		(Father 93504, Mother 93452)					
	1928	79	47	B45350	79	47	B45349
A94249 Male	1927	65		Bachelor	65	51	A93513
					65	9	A94247
	1928	75	6, 11	664751	75	11	B45350
					75	10	664751
	1929	86	25	B56490	86	21	B56490
B5640 Female	1927	Outfield	X12	Nestling			
		(Father 93692, Mother 93641)					
	1928						
	1929	92	74	B96418	92	70	B96418
	1930	100	59	C68910			
	1931	109	74	B97203	112	80A	?
	1932	124	74	B97203			
B45348 Female	1928				78	51	A38398
	1929	89	51	A38398	90	51	B97018
	1930	98	51	A38398			
B45350 Female	1928	79	47	A93573	75	11	A94249
	1929	Outfield	A178	?			
		Outfield	A235	B96328			
B56487 Male	1929	83	78	B96433	83	75	B96900
	1930	93	43A	B96433	93	43	C68705
	1931	113	47	C94217	113	54A	
B96282 Female	1929	Outfield	A58	Nestling			
		(Father ?, Mother A93448)					
	1930	101	80	C68252	Outfield	A8	B68424
B96433 Female	1929	83	78	B56487	85	30	B97007
	1930	93	43A	B56487			
B96446 Male	1929	Outfield	X19	Nestling			
		(Father ?, Mother ?)					
	1930	104	72A	C68563	104	72B	C68563
B97018 Male	1929	90	9	Bachelor	90	51	B45348
	1930	97	53	C68254			
		97	49	C68257	97	49	Bachelor
B97203 Male	1929	(Caught at banding station on August 11, probably a nestling)					
	1930						
	1931	109	74	B5640	109	59	Bachelor
	1932	124	74	B5640			
C68252 Male	1930	101	80	B96282			
	1931	111	80A	C94331	111	74	?
	1932	122	80	C94219	122	59	?
C68253 Female	1930	96	25	C68911			
	1931	106	25	C68801			
C68418 Male	1930	Outfield	A163	Nestling			
		(Father B96338, Mother B97451)					
	1931	114	34A	C94219	114	37	F45565
C68681 Female	1930	Outfield	A51	C68611			
	1931				110	59	F45857
C68801 Male	1930	95	47?	B96433	95	54A	C68257
	1931	106	25	C68253	106	25	Bachelor
C68910 Male	1930	100	59	B5640			
	1931	108	54A	F45359	108		Bachelor
	1932	119	49	F45947			
	1933	129	49	H18566	129	53	H18820
		129	49	F58248	129	51	F58248?

TABLE 5.—LIFE RECORD OF INDIVIDUAL BIRDS (*Continued*)

Band Number and Sex	Year	First Breeding Period			Second Breeding Period		
		Territory	Box	Mate	Territory	Box	Mate
C94219 Female	1931	114	34A	C68418			
	1932	122	80	C68252			
		120	53	F45994	(Female died)		
F45359 Female	1931	108	54A	C68910			
	1932	116	40A	F58648			
	1933	Outfield	A164	F45764	Outfield	A164	F45764
F45763 Male	1931				Outfield	A260	Nestling
					(Father 45764, Mother C68978)		
	1932				121	49	F45947
F45942 Female	1932	117	25	F45946	117	26?	F45946
	1933	128	25	H18582			
F45946 Male	1932	117	25	F45942	117	26	F45942?
	1933	130	21A	H18566	130	92	
F45987 Male	1932	118	54A	F45992	118	54A	F45992?
	1933	134	54A	H18587	134	54A	H18587
	1934	144	43A	L24955	144	75	L24955
	1935	157	75	L24955	157	43A	L24955
	1936	169	47	L73248	169	37	L73248
					169	34A	34-86014
	1937	177	34	36-38389	(Leg broken, amputated)		
F58248 Female	1932	Outfield	A7	Nestling			
		(Father ?, Mother F58244)					
	1933	129	49	C68910	129	51?	C68910
F58493 Female	1932	Outfield	A310	Nestling			
		(Father F58302, Mother F45477)					
	1933	132	74	H18570	Outfield	A7	F58309
F58648 Male	1932	116	40A	F45359			
	1933	136	43	H18584			
		136	40A	H18900	136	34A	A18900
	1934	142	37	L24950			
F58955 Female	1932	Outfield	A201	Nestling			
		(Father C94427, Mother F58103)					
	1933	127	11	H18600			
H18600 Male	1933	127	11	F58955	127	11, 6	Bachelor
	1934	141	25	L24101	141	21A	Bachelor
L24101 Female	1933	135	43A	L24102			
	1934	141	25	H18600	146	49	L24996
	1935	153	25	L24956	160	49	L24996
	1936	166	21A	L24949	170	75	35-13603
L24102 Male	1933	135	43A	L24101			
	1934	138	3A	L24948			
L24944 Female	1934	148	73	L24946	149	73	?
	1935	161	63	34-4020	Outfield	A8	?
L24946 Male	1934	148	73	L24944	Outfield	A7	34-3502
	1935	Outfield	A10	34-4919			
	1936	165	10, 11	Bachelor	165	3A	Bachelor
L24949 Male	1934	150	91	L24951	150	54A, 47	Bachelor
	1935	158	72	?	158	75	Bachelor
	1936	166	21A	L24101	166	11	35-13604
	1937	178	40A	36-38381	178	37	36-38381
					178	34	36-38389
L24951 Female	1934	150	91	L24949			
	1935						
	1936	171	79	34-86997	168	47	34-86015
	1937	180	43A	35-13603			
L24955 Female	1934	144	43A	F45987	144	75	F45987
	1935	157	75	F45987	157	43A	F45987

TABLE 5.—LIFE RECORD OF INDIVIDUAL BIRDS (*Concluded*)

Band Number and Sex	Year	First Breeding Period			Second Breeding Period		
		Territory	Box	Mate	Territory	Box	Mate
L24956 Male	1934	139	10	Bachelor			
	1935	153	25	L24101	152	92	34-4201
L24996 Male	1934	146	53, 49	Bachelor	146	49	L24101
	1935	160	53	?	160	49	L24101
L73248 Female	(Banded elsewhere)						
	1936	169	47	F45987	169	37	F45987
34-4020 Male	1934	Outfield	A104	34-4021			
	1935	161	63	L24944	161	59	Bachelor
34-4201 Female	1934	Outfield	A66	?			
	1935	Outfield	A10	?	153	92	L24956
	1936	Outfield	A256	?			
34-4445 Female	1934				Outfield	51	Nestling
					(Father 34-4419, Mother 34-4405)		
	1935	159	47	34-86013	154	25	34-86085
34-86014 Female	1935	155	40A	34-86015	156	34A	34-86088
	1936	168	40A	34-86015	169	34A	F45987
34-86015 Male	1935	155	40A	34-86014			
	1936	168	40A	34-86014	168	47	L24951
	1937	184	53	36-38811			
	1938	197	43A	38-1607			
34-86767 Male	1935				Outfield	A142	Nestling
					(Father F58297, Mother 34-3792)		
	1936						
	1937				176	25	37-93972
34-86997 Male	1936	171	79	L24951	171	43	35-13653
	1937						
	1938				200	40A	36-38389
35-13603 Male	1936	170	43A	35-13604	170	75	L24101
	1937	180	43A	L24951	180	43A	Bachelor
	1938	201	34	36-38811	201	34	36-38811
35-13700 Male	1937	186	72A	36-38388	Outfield	A9	35-13913
	1938	191	69	38-1662			
36-38040 Female	1936	Outfield	A7	Nestling			
		(Father ?, Mother 35-13528)					
	1937	182	47	36-38856	182	47	36-38856
	1938	196	47	36-38856	196	47	36-38856?
	1939	213	79	36-38856	213	43A	36-38856
36-38389 Female	1937	177	34	F45987	178	34	L24949
	1938	199	37	38-1654	200	40A	34-86997
36-38426 Female	1938				195	54A	36-38427
	1939	208	49	36-38429			
36-38427 Male	1938				195	54A	36-38426
	1939	205	11	Bachelor	205	11	36-38462
36-38429 Male	1938				189	3A	36-38428
	1939	208	49	36-38426			
36-38804 Male	1937	173	10	Bachelor	Outfield	A8	35-13529
	1938				Outfield	A14	38-1863
36-38811 Female	1937	184	53	34-86015			
	1938	201	34	35-13603	201	34	35-13603
					202	9	38-1681
36-38856 Male	1937	182	47	36-38040?	182	47	36-38040
	1938	196	47	36-38040	196	47	36-38040
	1939	213	79	36-38040	213	43A	36-38040
37-93876 Male	1937				Outfield	A302	36-38569
	1938				194	51A	38-1642
38-1607 Female	1938	197	43A	34-86015	198	75	38-1684
	1939				204	10	36-38461

X. SUMMARY

THE TERRITORIAL behavior of 142 male and 147 female house wrens over a period of nineteen years on a fifteen-acre estate is here described. Additional information obtained from nesting activities at approximately three hundred boxes on outlying estates is collated. Case histories of 215 territories are presented, along with maps of most of the territories to show variations in boundary and size. A condensed history of 98 birds in respect to territories, boxes, and mates is given to show changes between breeding periods and from one year to another.

Although first-year birds may be among the first to arrive in late April and early May, adults of two or more years of age make up a far greater percentage of the migratory population at this time than they do later in the season. Females arrive about nine days later than the males.

Adult males that have previously nested almost invariably return to the same territory that they formerly occupied, or they establish a new territory adjacent to it. The return of adult females to their former nesting areas is almost as regular.

With young birds hatched the preceding season, there is a marked tendency to scatter in all directions, although they occur in greatest relative numbers in the vicinity where they were hatched.

Only the male bird sings, and his songs are classified into three types. The "territory" song serves to notify other males that the area is occupied, to advertise the male's presence to the females, and to entice the female to enter his particular territory. The "mating" song expresses great sexual excitement and may be stimulating to the female for coition. The "nesting" song serves to remind other birds that the territory is occupied and aids in coordinating the activities of male and female around the nest. Both sexes have a variety of call-notes for expressing various emotional states and for intercommunication. Movements of wings and tail are used for the same purpose.

A male usually possesses two or three nest-sites in his territory and occasionally as many as seven. This gives incoming females a variety of choice for beginning a nest and aids the male in retaining her as his mate. Any one of the nest-sites may be used for a second brood later in the season or for two simultaneous nestings with different females. Their location helps to establish the outline and size of the territory.

Territories are established and defended by singing, by taking possession of nest-sites, by assuming threatening postures sometimes accompanied with scolding, by chasing, and by physical combat. This order is one of increasing exertion and energy demand and may represent the reverse order of steps through which the territorial behavior has developed in the course of evolution.

In the establishment of nest-sites, house wrens may destroy the nests, eggs, or young of the same or of different species, or even other adult birds. Although there is considerable individual variation in this aggressive behavior, it tends to be most intense during years when the total house wren population on the area is highest.

The female does not defend territory nor recognize the limits of territory as established by the male. When the female appears confined to a territory, it is due to her nest-box being centrally located within the territory, to her being chased out of neighboring territories, or to the male's adjustment of the outlines of his territory to coincide with her movements. The presence of an unmated female is a potent stimulus to the male for establishing territories or modifying their former boundaries or of competing with his neighbors.

Territorial boundaries are frequently in a state of flux and rarely remain uniform throughout the season. These changes are caused by early arriving males attempting to take possession of very large territories, parts of which they are forced later to yield, to the impact of new males arriving and carving out territories, to variations in the activity and feeding areas of the female mate, to the shifting population of both males and females between the first and second breeding periods and the necessity for remating, and in general, to variation in activities and relations of established males on adjacent territories.

Territories in the Hillcrest area average 1.0 acre (0.4 hectare) in size, but they vary all the way from less than 0.25 to 3.6 acres (0.1-1.44 hectares). The size of the territory varies inversely with the size of the house wren population and does not exert a limiting influence on the total numbers of the species in the area until it approaches the minimum compressible limit. The adult birds restrict their intensive daily activity to limited parts of the territory but eventually cover the entire area.

There is a non-breeding population of house wrens which in the males varies from 28 to 35 per cent of the total male population and in the female from 13 to 20 per cent of the total female population. Various levels of reproductive activity exist as represented in different birds: no attempt at breeding at all, temporary and unsuccessful splurges at nesting activities, maintenance by the male of a territory throughout a breeding period or the entire season but without obtaining a mate, securing a mate and a nest for one period only, the undertaking of a nesting during both breeding periods, and perhaps finally polygamy. Polygyny occurs in about six per cent of all matings, but multiple nesting by the female is rare. First-year birds on the average have a lower reproductive vigor than do birds that have nested before.

The successful mating of two birds of opposite sex appears to depend on their physiological and psychological readiness, their ability to stimulate each other sexually, the location and character of the territory, the location and character of the nest-site together with the nest foundation begun by the male, and finally their freedom from other activities.

Except for the fact that only the male sings, sex recognition is based on differences in behavior of the two sexes. Later, there may be recognition of each other as individuals through characteristic mannerisms.

Mating for a second brood follows the same pattern as for the first brood, even though 40 per cent of the second matings are with the same individuals. Remating of a pair for a second brood is aided by possibly their physiological condition and behavior patterns being already adjusted to each other, by the male aiding the female in the care of the first brood, which duty, however, he assumes only about half of the time, and by both birds returning to the same territory. Remating of a pair the following year occurred in 42 per cent of the cases where both birds of the pair survived and returned to the locality: this remating being dependent upon both birds returning to their former or to adjacent territories and to neither being already mated at the time the other arrives.

Territory is maintained throughout each breeding period and breeding season, although there may be some decrease in activity as nesting progresses. This continuance of territory may be correlated with the tendency toward polygyny manifest in the male, with the use of the same territory for later matings, and it may also involve the need for a constant and readily available source of food and for freedom from annoying intruders. Primarily, however, the territorial behavior is most closely linked with the acquiring of a first mate. There is no evidence that territory is maintained at any other than the breeding season of the year.

XI. LITERATURE CITED

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ILLINOIS BIOLOGICAL MONOGRAPHS

VOL. XVIII   No. 4

EDITORIAL COMMITTEE

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THE MORPHOLOGY, TAXONOMY, AND BIONOMICS OF THE NEMERTEAN GENUS CARCINONEMERTES

WITH FOUR PLATES AND ONE MAP

BY

ARTHUR GROVER HUMES

CONTENTS

ACKNOWLEDGMENT

INTRODUCTION

ALTHOUGH all animals at some time in their life histories come in contact
with other animals, only a relatively small number become so intimately
associated with other species that the latter change from an incidental
part of the environment to become an indispensable element of it. The
innumerable varieties and degrees of intimacy between animals of differ-
ent species, extending all the way from the condition of free life to the
most dependent type of endoparasitism, defy exact classification. Great
interest is attached to animals which live in relationships with each other
intermediate to free-living and parasitic ways of life. The morphological
modifications present in animals of these various types of associations
(commensalism, symbiosis, inquilinism, phoresy, ectoparasitism, etc.)
illustrate forcibly the presence of evolutive forces in living cells and the
influence of the environment. However, as Caullery (1922) pointed out,
the random diversity of the deformations in such animals shows that the
evolutive changes are conditioned by the intrinsic properties of the living
forms. Our knowledge of the expression of forces at work in animal
evolution has been increased by observations on the morphology of
animals which are to a greater or lesser degree dependent on individuals
of other species. Accurate and detailed information on many groups,
however, is still lacking.

Very little is known about those nemertean worms which live in close
associations with other animals. Some authors have even been led to
make gross misstatements concerning them. Parker and Haswell (1910,
p. 296) stated that "one nemertean lives *in the interior* of a crustacean
and is probably a true parasite" (italics mine). In reality the nemertean
referred to lives only as an ectohabitant on the external surface of the
exoskeleton. The best known genus of nemerteans which is not free-
living is Malacobdella, a form which inhabits the mantle cavities of
various lamellibranchs. Even for this genus, however, our understand-
ing of the taxonomy, distribution, life history, and host relationships is
only fragmentary. Likewise, the genus Carcinonemertes, the members of
which are ectohabitants of crabs, has been to date much neglected.
Further studies on the genus Carcinonemertes seemed to the writer to be
necessary if only because of the rarity of parasitic and commensal
species in the phylum Nemertea. Moreover, a knowledge of the form
and function of these animals may eventually be useful in interpreting
the phylogenetic evolution of parasitism in the group.

Preliminary observations on Carcinonemertes at Grand Isle, Louisiana,
and a survey of the previous literature on the genus indicated that
several lines of investigation needed to be carried out. In the first place,
no adequate description of *Carcinonemertes carcinophila* (Kölliker), the

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first species to be described and the type species, existed in the literature. Secondly, although Takakura (1910) mentioned a unique dorsal duct in male specimens of *Carcinonemertes mitsukurii* Takakura, his work, having gone unnoticed by other students of the nemerteans because of its publication in Japanese, needed to be made generally available for study. Especially was this true since a similar dorsal duct was found by the writer in *C. carcinophila*. Because of the uniqueness of the dorsal duct the writer felt that a detailed description of the duct as it exists in the genus Carcinonemertes should be given. In the third place, the life history of *C. carcinophila* could now, with the information given by Churchill (1919) and Gray and Newcombe (1939) regarding the life history of the host crab and with the data collected by the writer, be interpreted more fully. In the fourth place, the writer found that by collecting specimens of Carcinonemertes from the egg masses of crabs available in museum collections, new data on the distribution of the genus and the various species of crabs infested could be collected. Lastly, taxonomic considerations, involving the description of a new species and a new variety and the diagnosis of the family Carcinonemertidae, demanded a restudy of the genus. Investigations along these five principal lines have been undertaken, and the results are given in the following pages.

MATERIALS AND METHODS

THE WORMS used in this study came from two sources. The specimens of *C. carcinophila imminuta* from Grand Isle, Louisiana, were collected alive by the writer during the summers of 1939 and 1940. All other specimens were obtained from the egg masses of ovigerous crabs in the collections of the Museum of Comparative Zoology, Cambridge, Massachusetts, and the United States National Museum, Washington, D. C.

The crabs were obtained at Grand Isle by an otter trawl, by minnow seines, or by hand, and brought into the laboratory before examination for worms was made. Ovigerous crabs were kept in sea water until they could be examined. In this way most of the worm eggs and larvae and immature worms remained in the egg masses in good condition. The non-ovigerous crabs were usually left without water, since in this way they survived better in the relatively high temperatures of the laboratory. In no case did examination occur later than twelve hours after capture.

The crab gills and egg masses if present were removed and placed in separate finger bowls of sea water. Most of the worms which were in capsules between the gill lamellae left the gills within a few hours and congregated on the side of the dish farthest from the source of light. There they could be picked up in a pipette and transferred to clean sea water or to fixative. The transfer had to be made quickly or the worms

adhered to the inside of the pipette. The egg cords of the nemerteans were picked off the egg masses either with the aid of a binocular or without magnification after the eye had become accustomed to their appearance. The free-swimming larvae left the egg masses in a few hours and collected on the side of the finger bowl nearest the source of light, where they were pipetted off into another dish. Very young worms were often found crawling among the debris on the bottom of the dish and along the sides. Mature females were recognized by their relatively greater length and reddish coloration. Mature males, on the other hand, were found to be shorter and whitish rather than red.

Before making measurements of the live worms the specimens were usually first anaesthetized by dropping a few crystals of chloretone into the dish or by placing the dish in a closed chamber with chloroform fumes.

Most of the worms were fixed in either Schaudinn's or Bouin's fluid. The live worms were studied either whole or by maceration. Vital stains, including Bismarck brown, neutral red, methylene blue, and Nile blue sulphate, were useful in accentuating some details of the anatomy. Orange G was especially useful in staining the basis. Nearly all the observations and measurements of the minute structures were made under an oil immersion objective and a 10x ocular.

Many of the worms recovered from crabs in museum collections had been in 70 to 80 per cent alcohol for years. One collection from *Ovalipes ocellatus* (Herbst) had been immersed thus for 89 years. Nearly all of these worms were still inside their mucous sheaths. It was found that with ordinary dehydration in ethyl alcohol and clearing in xylol the worms became very brittle and sectioned poorly. The following technique was then adopted, after experimentation showed that it produced usable sections, even though the worms had been poorly fixed:

50% ethyl alcohol	2 hours
35% ethyl alcohol	2 hours
35% ethyl alcohol + 2 drops of Labarraque's solution	10 minutes
50% ethyl alcohol	2 hours
5 cc HOH + 4 cc ethyl alcohol + 1 cc n-butyl alcohol	2 hours
3 cc HOH + 5 cc ethyl alcohol + 2 cc n-butyl alcohol	2 hours
1.5 cc HOH + 5 cc ethyl alcohol + 3.5 cc n-butyl alcohol	3 hours
0.5 cc HOH + 4 cc ethyl alcohol + 5.5 cc n-butyl alcohol	5 hours
2.5 cc ethyl alcohol + 7.5 cc n-butyl alcohol	7 hours
n-butyl alcohol (undiluted)	10 hours
change of n-butyl alcohol	10 hours
n-butyl alcohol + paraffin at melting point (1:1)	10 hours
paraffin slightly above melting point	2 hours
change of melted paraffin	30 minutes

The worms were sectioned 10 μ in thickness and mounted in the usual manner. At first, safranin followed by fast green as a counterstain was used to stain the sections. By this technique the basis and the nuclei were

stained red, while the fast green colored the basement membrane and the cytoplasm green. However, because of the poor fixation these two stains did not stain the tissue evenly. A more satisfactory stain was Heidenhain's iron haematoxylin, which stained the basis and the nuclei black. The muscle fibers were stained a dark gray by this technique, although here, as with the safranin and fast green, the stain did not color the tissue evenly. Although the contents of the gland cells stained a light pink with safranin, they were unstained with the iron haematoxylin.

The live worms, after being fixed, were washed free of the fixing agent, dehydrated in increasing concentrations of ethyl alcohol, and cleared before embedding in xylol or in cedar oil. The latter clearing agent was found to be far superior, in that it preserved the contents of the intestine, the ocelli, and the cellular details much better. These worms were cut from 4 μ to 10 μ in thickness. The most convenient thickness, in respect to ease in cutting and usefulness in identifying structures, was 7 μ. The sections were stained with safranin and fast green, as mentioned above, with Delafield's haematoxylin, Heidenhain's iron haematoxylin, or rarely with Mallory's phosphotungstic acid haematoxylin. Methylene blue stained only the mucus in the submuscular and cephalic glands. Sections stained with methylene blue and counterstained with eosin showed bright blue glands against a pink background. Feulgen's nucleal reaction, when used on the sectioned Schaudinn-fixed material, was useful in identifying nuclei. In this case fast green was used as a counterstain against the red nuclei.

A few whole mounts stained with Delafield's haematoxylin were prepared, but were too opaque to be of much use.

CARCINONEMERTES CARCINOPHILA (KÖLLIKER) VAR. *CARCINOPHILA* (KÖLLIKER)

HISTORICAL ACCOUNT

DURING the voyage of the Astrolabe in the years 1826-1829, Quoy and Gaimard (1833) found in a barnacle at Amboina a nemertean which they named *Borlasia quadripunctata*. This slender, slightly flattened worm was about two inches long and white, except for two longitudinal brown lines on the dorsal side, the space between being yellow. The head was obtuse, a little indented in front, with no sign of separation from the body. On the dorsal side of the head there were four round, black spots. The mouth was a long terminal slit. From this brief description Coe (1902a) thought it probable that the worm belonged to the genus Tetrastemma. No one else has since found such a worm.

This record constitutes the earliest mention in the literature of a crustacean and a nemertean living in any kind of an association.

It was not until 1845 that a nemertean living on crabs was discovered. Kölliker (1845) found six nemerteans living on the egg masses of a small crab at Messina, Sicily. These he named *Nemertes cartinophilos,* giving the following description: "Länge 1-3 Linien. Farbe blassorange. Augen zwei, elliptisch. Darmanhänge kurz, zahlreich. Rüssel sehr kurz, mit einem styletartigen Zahl von 0.013''' versehen. Körper der Samenfäden 0.009''' lang." Von Siebold (1850, p. 382) referred very briefly to Kölliker's species as *Nemertes carcinophilos,* changing the "t" to a "c" to correct an obvious misprint. Modern writers have used the corrected spelling, in accordance with Article 19 of the International Rules of Zoological Nomenclature.

Van Beneden (1861) described a nemertean, *Polia involuta,* which he considered to be a new species, evidently unaware that Kölliker had sixteen years before described the same worm as *Nemertes carcinophilos.* Van Beneden later (1876, pp. 46 and 81) pointed out the priority of Kölliker's name. Van Beneden's description is rather short and contains little that is not much better shown by later authors, especially McIntosh and Coe. His description of the embryology is the first to be found in the literature on the genus Carcinonemertes. The worm has a direct type of development, with no special larval stages such as the pilidium or the larva of Desor. The fertilized and developing eggs are placed in rows in mucous sheaths, much like those in which the adults live, but without the flagstone-like pieces on the surface. The embryo develops cilia before leaving the egg case. The free-swimming ciliated larva has an anterior, and sometimes also a posterior, flexible cirrus or filament which whips about as the larva swims. The skin becomes more and more distinct, while the yolk material passes to the posterior half of the larva to take part in the formation of the intestine. Two minute ocelli are present on the larva. Van Beneden stated that the long filaments at the ends of the larva are shed, and possibly also the entire ciliated covering, though the latter point is not clear. The larva in its shedding process was compared with the miracidium of the Trematoda or the hexacanth of the Cestoda. This comparison is not a good one, for, as will be seen later, the larva of Carcinonemertes is provided with rudiments of nearly all the adult organs, except possibly the gonads.

In 1862, Diesing listed *Cephalothrix involuta* (Van Beneden), which he indicated to be identical with *Polia involuta* Van Beneden, and also *Nemertes carcinophila* Kölliker, not recognizing the synonymy of the two names.

Eight years after Van Beneden's description of *Polia involuta,* McIntosh (1869) described in greater and more exact detail its anatomy and

development. McIntosh was aware of Kölliker's work, since he referred after *Polia involuta* Van Beneden in a footnote to *Nemertes carcinophilus* Kölliker. No reason was given for continuing to use Van Beneden's name, when the worm described by the latter as *P. involuta* was clearly the same species as *N. cartinophilos* Kölliker 1845. The areolar sheaths attached to the bases of the abdominal appendages of ovigerous female crabs, *Carcinides* (= *Carcinus*) *maenas* (Linnaeus), were described and a good description of the proboscis and head region given. The absence of the proboscis sheath and the rhynchocoel with its fluid was mentioned briefly. His description of the anterior region and the development of the young worms is accompanied by drawings which, for the first time, indicate something of the histology of the proboscis, the whole head, the early egg, and the ciliated free-swimming larva.

McIntosh (1873-1874) wrote an extensive monograph on nemerteans published by the Ray Society of London. In this the name *Polia involuta* Van Beneden was discarded in favor of *Nemertes carcinophila* Kölliker. Included in the monograph is a synonymy and brief description of this species, which he found on *Carcinides* (= *Carcinus*) *maenas* (Linnaeus) at St. Andrews, Scotland. His remarks on the internal anatomy and development were repeated verbatim from his 1869 paper. In addition to the 1869 figures there is a colored figure of the whole worm. The drawing of the anterior region of the body has the blood vessels shown in blue.

Another nemertean from a decapod crustacean at Messina, Sicily, was reported by Dieck (1874). This worm, named by him *Cephalothrix galatheae*, occurred in the egg masses of an anomuran, *Galathea strigosa* Linnaeus. Dieck apparently knew nothing of Kölliker's previous work. Coe (1902a) has critically evaluated this species and concluded that it very probably is synonymous with *Nemertes carcinophila* Kölliker. The general body form (size, shape, color, ocelli, absence of cephalic furrows and cerebral sense organs), the eggs and developmental stages, the occurrence in the same locality (Messina), and the presence of internal fertilization all show great similarity to Kölliker's worm. Bürger (1897-1907) disagreed with Coe's interpretation and argued that Dieck's species should be considered distinct, inasmuch as it was described as having the mouth behind the brain, a proboscis without a stylet, and the lateral nerve cords enclosed in the body muscle layer. The writer feels that the decision regarding the specific identity of these two worms should be postponed until additional specimens of *Cephalothrix galatheae* (if such a species exists) can be obtained.

Willemoes-Suhm (1874) found a parasitic nemertean on the ventral side of the abdomen of a Gulf-weed crab, *Planes* (= *Nautilograpsus*) *minutus* (Linnaeus), between the Azores and Bermuda. This was de-

scribed as small, brownish, two millimeters in length, with a very short proboscis. Two pairs of eyes were present, the second only punctiform. In his figure 4, Willemoes-Suhm showed two accessory stylet pouches, each having two or three minute stylets. These were not mentioned in the text. This worm was later called *Prostoma suhmi* by Bürger (1897-1907). Since the specimens of this worm were lost during the voyage of the Challenger, Hubrecht (1887), while studying the nemerteans collected on that famous voyage, was unable to determine anything further. It is possible that the worm was a free-living species which accidentally was present on the abdomen of the crab. When a batch of Sargassum weed is hauled up out of the water to be examined, many of the animals are apt to be uprooted and transplanted to unnatural situations.

The embryology of the Nemertea was considered by Barrois (1877) in some detail. He concluded that two chief types are present, the one comprising the pilidium and the larva of Desor, and the other the direct development and the so-called "planula." The development of *Polia carcinophila* (Kölliker) (= *Nemertes carcinophila* Kölliker) was shown to be of the direct type. The larva is a nemertean already formed and has nothing comparable to a "planula." The development of this species resembles closely that of *Amphiporus lactifloreus*. The chief difference is that the young nemertean when hatched, instead of adopting the adult way of life, starts to swim freely in the water. The differentiation of the musculature occurs in *P. carcinophila* before the peripheral epithelium is separated completely from the white deutoplasmic mass in the center of the embryo. Barrois was unable to tell whether the free-swimming larva sheds its skin before changing from a swimming to a crawling way of life. Van Beneden (1861) for *Polia involuta* (= *Nemertes carcinophila*) and Dieck (1874) for *Cephalothrix galatheae* both affirmed that the ciliated skin is shed, but McIntosh (1869) denied this. According to Barrois the newly hatched larva shows a clearly indicated proboscis, a structure which McIntosh mistook for the esophageal region. Even in the unhatched embryos a vague rudiment of the proboscis may be visible. In the young larva the proboscis is a hollow structure but unarmed. The body is covered with cilia and there are long apical flagella at both ends. As the worm grows, the armature of the proboscis appears. There is no proboscis sheath, the proboscis floating free in the cavity of the body above the intestine. The lateral organs are absent.

Carus (1885) placed Dieck's species in the genus Carinella as *Carinella galatheae* (Dieck), and stated that it is perhaps synonymous with *Nemertes carcinophila* Kölliker. He listed the latter species separately however. *Polia involuta* Van Beneden he regarded as a synonym of *Nemertes carcinophila* Kölliker.

Hubrecht (1887) quoted from the journal of Willemoes-Suhm a brief

description of the worm from *Planes minutus* (Linnaeus). However, this description contains no information beyond that given in the 1874 paper, except that the stylet lies just behind the ganglia, which are large. Braun (1888) mentioned *Nemertes carcinophila* Kölliker and *Cephalothrix galatheae* Dieck (which he held to be separate species) and summarized some of the previous work on these worms.

Female specimens of *Xantho floridus* Mont. at Concarneau, France, were found by Giard (1888) to be infested with a small nemertean, which he called *Polia xanthophila*, giving no description or diagnosis of any kind. Ovigerous specimens of *Carcinides* (= *Carcinus*) *maenas* (Linnaeus) were infested at Wimereux (about 300 miles northeast of Concarneau) with a worm which Giard identified as *Polia involuta* Van Beneden (= *Nemertes carcinophila* Kölliker). It is very probable that the worms in the two localities were the same species. In 1890 Giard again recorded the presence of *Nemertes carcinophila* Kölliker at Wimereux, and noted its synonymy with *Polia involuta* Van Beneden. He found the worms very common in the spring on the eggs of *Carcinides* (= *Carcinus*) *maenas* (Linnaeus). Joubin (1890) found *Nemertes carcinophila* Kölliker on *Carcinides maenas* at Roscoff, France. A male and a female were often found in the same mucous sheath and sometimes were folded two or three times in respect to length. He did not find Dieck's species, which he regarded as *Carinella galatheae* (Dieck), although the host, *Galathea strigosa* Linnaeus, was common there.

Van Beneden (1883) recorded *Polia involuta* Van Beneden (= *Nemertes carcinophila* Kölliker) at Ostende, Belgium.

While making a survey of the nemerteans of Plymouth Sound, England, Riches (1893-1895) did not find *Nemertes carcinophila*, although he examined ovigerous *Carcinides maenas*. He cited McIntosh as having stated that these worms had been found only at Messina, Sicily, and on the coast of Belgium, not in England. He was evidently unaware of the fact that McIntosh had found *Nemertes carcinophila* at St. Andrews, Scotland, in 1869. Riches also examined several ovigerous *Galathea strigosa* Linnaeus, but found none of Dieck's *Cephalothrix galatheae*.

In his famous monograph of the nemerteans of the Gulf of Naples, Bürger (1895) mentioned *Eunemertes carcinophila* (Kölliker) and cited McIntosh's (1873-1874) description and figures. Attention was called by him to the fact that McIntosh, Pl. 12, fig. 14, showed the main stylet half as long as the basis.

Richard (1899) listed four species of nemerteans found on Crustacea. They were *Eunemertes carcinophila* (Kölliker), *Eunemertes xanthophila* (Giard), *Carinella galatheae* (Dieck), and *Tetrastemma fuscum* Willemoes-Suhm (= *Prostoma suhmi* Bürger).

A nemertean on crabs in North America was reported in the literature for the first time by Coker (1901). He mentioned that among the inhabitants of the gill chambers of *Callinectes sapidus* Rathbun at Beaufort, North Carolina, there were "vorticellid colonies and acinetid Protozoa, Polyzoa—ectoproctous and endoproctous—nemerteans, etc." This is also the first record of any nemerteans from the blue crab *Callinectes sapidus*. No details regarding these nemerteans were given, although they were undoubtedly *Carcinonemertes carcinophila* (Kölliker), since this species has since been found in the same locality.

In 1902, Coe published a paper on the nemertean parasites of crabs, in which he summarized, evaluated, and reorganized the previous work on the group. In it, a new genus, Carcinonemertes, and a new species, *Carcinonemertes epialti*, were described and a redescription of *Carcinonemertes carcinophila* (Kölliker) was given. Coe mentioned that Professor J. P. McMurrich in correspondence stated that he had found nemerteans among the egg masses of the lady crab, *Ovalipes* (= *Platyonichus*) *ocellatus* (Herbst), in July, 1889. He pointed out that this was the first observation of a nemertean living on a crab in this country, though no definite locality was given. This unpublished note preceded Coker's paper in time.

Coe's paper (1902a) constitutes the first piece of work ever done on New World nemerteans living on crabs. He found on *Platyonichus ocellatus* (Herbst) (= *Ovalipes ocellatus ocellatus* (Herbst)) at Cape Cod, Massachusetts, a nemertean which he regarded as identical with the previously described European species, *Nemertes carcinophila* Kölliker. For this he erected his new genus, inasmuch as the anatomical structures were so decidedly different from those of Eunemertes in which the worm had been placed by Joubin and by Bürger. Some details regarding the development and life history of the genus were included in the paper. In the same year Coe (1902b) republished his generic description of Carcinonemertes and rediagnosis of *C. carcinophila* (Kölliker). In 1904b (pp. 150-154) and 1905a (pp. 230-233) Coe repeated his original (1902a) descriptions of the genus Carcinonemertes.

Bürger (1897-1907), on page 530 of his extensive discussion of the Nemertea, mentioned *Carcinonemertes carcinophilon* (Kölliker), using the ending *-on* instead of either the original *-os* or the *-a* of later authors.

In their list of the fauna of Woods Hole (1913), Sumner, Osburn, and Cole mentioned (p. 591) *Carcinonemertes carcinophila* (Kölliker) from Nobska Point, Katama Bay, and Nememsha Bight, Massachusetts. A new family name, Carcinonemertidae, was used, evidently for the first time and without diagnosis of any kind. Most other authors since Coe's description of the genus have placed it in the family Emplectonematidae Bürger (1904).

Shipley (1926) in a brief discussion of the parasitic nemerteans suggested that those living on Crustacea, like Malacobdella, which lives in the mantle cavities of marine clams, have "an organ of attachment, a sucker, a feature unknown in the free-living forms . . . . the alimentary canal has no lateral pouches, but as a compensation it is longer than the body, and coiled." It is easy to see that he was here describing Malacobdella and not Carcinonemertes. The description created an erroneous idea of the so-called parasitic nemerteans as a group.

Pearse (1932) found in the gill lamellae of *Bathynectes superba* (Costa), taken 20 miles south of Tortugas, Florida, in 155 fathoms, worm-like parasites containing two lateral, pigmented spots near the anterior end. *Portunus spinicarpus* Stimpson from the Gulf Stream in 60 fathoms of water was reported by the same author to be infested in the gill lamellae by "worms with the lateral eye spots." These were verified as *Carcinonemertes carcinophila* (Kölliker) by Dr. A. S. Pearse and reported as such in conversation with the writer in Philadelphia, Pennsylvania, on January 1, 1941.

In correspondence of June 16, 1940, Dr. Wm. E. De Turk stated that he had found nemerteans (later identified by Dr. W. R. Coe as *C. carcinophila*) on *Portunus spinimanus* Latreille, *Ovalipes ocellatus ocellatus* (Herbst), *Ovalipes ocellatus guadulpensis* (Saussure), *Callinectes sapidus* Rathbun, and *Callinectes ornatus* Ordway, all at Beaufort, North Carolina. He reported finding larvae (by which he no doubt meant immature worms) on both sexes of the hosts.

SPECIFIC DESCRIPTION

The synonymy of *Carcinonemertes carcinophila carcinophila* (Kölliker, 1845) Coe, 1902, is as follows:

1845 *Nemertes cartinophilos* Kölliker. Verhandl. Schweiz. Naturf. Gesellsch. 29: 86-98.
1850 *Nemertes carcinophilos* Kölliker. Von Siebold, Arch. f. Naturgesch. 16:351-468.
1861 *Polia involuta* Van Beneden. Mem. Acad. roy. Sci. Belg. 32:1-56.
1862 *Cephalothrix involuta* (Van Beneden). Diesing, Sitzb. kais. Akad. Wiss. Wien 45:191-318.
1862 *Nemertes carcinophila* Kölliker. Diesing, ibid.
1869 *Nemertes carcinophilus* Kölliker. McIntosh, Trans. Roy. Soc. Edinb. 25:305-433.
1869 *Polia involuta* Van Beneden. McIntosh, ibid.
1873-1874 *Nemertes carcinophila* Kölliker. McIntosh, Monogr. Brit. Annelids, part 1, pp. 1-213.
1874 *?Cephalothrix galatheae* Dieck. Jen. Zeitschr. f. Naturw. 8:500-520.
1877 *Polia carcinophila* (Kölliker). Barrois, Ann. Sci. nat. (6) 6:1-232.
1883 *Polia involuta* Van Beneden. Van Beneden, E., Bull. Acad. roy. Belg. (3) 6:458-483.
1885 *?Carinella galatheae* (Dieck). Carus, Prodromus Faunae Mediterranneae, vol. 1.
1888 *Polia xanthophila* Giard. Bull. sci. Fr. et Belg. 19:492-513.

1890 *?Carinella galatheae* (Dieck). Joubin, Arch. Zool. exp. et gén. (2) 8:416-602.
1890 *Eunemertes carcinophila* (Kölliker). Joubin, ibid.
1895 *Eunemertes carcinophila* (Kölliker). Bürger, Fauna u. Flora d. Golfes von Neapel 22:1-743.
1895 *Emplectonema carcinophila* (Kölliker). Verrill, Trans. Conn. Acad. Arts and Sci. 9:523-534.
1899 *Eunemertes xanthophila* (Giard). Richard, Arch. de Parasitol. 2:548-595.
1902 *Carcinonemertes carcinophila* (Kölliker). Coe, Amer. Naturalist 36:431-450.
1902 *Carcinonemertes carcinophila* (Kölliker). Coe, Zool. Anz. 25:409-414.
1904 *Emplectonema carcinophilon* (Kölliker). Bürger, in Schulze, "Das Tierreich," part 20, pp. 1-151.
1897-1907 *Carcinonemertes carcinophilon* (Kölliker). Bürger, in Bronn, "Klass. u Ord. des Tierreichs," 4 (suppl.):1-542.

Kölliker's original description is very brief. In translation it is as follows: "Length 1-3 lines. Color pale orange. Two elliptical eyes. Intestinal pouches short, numerous. Proboscis very short, provided with a stylet-like tooth 0.013‴. Bodies of the spermatozoa 0.009‴ long. Six of these worms of different sizes were found at Messina in the egg masses of a small crab." Converting the measurements in lines (see Behrens, 1908) to the metric system now used, the length is 2.1 to 6.3 mm, the stylet-like tooth is 27.5 μ, and the bodies of the spermatozoa are 19 μ.

Later writers (Van Beneden 1861, McIntosh 1873-1874, and Bürger 1895) have redescribed the worm under various names (see synonymy above). The rediagnosis of the species by Coe (1902a) is the most exact. This in brief is as follows: The body is slender, 6-15 mm long when on the gills and 20-70 mm when sexually mature. The color is yellowish orange, pale reddish, rose pink, or bright brick red. The posterior proboscis chamber is very small and rounded. The central stylet lies immediately posterior to the brain, when the worm is in the ordinary states of contraction. The slender basis measures about 25-30 μ in length by 6-8 μ in average diameter. The central stylet is about 8-12 μ long, or about ⅓ to ½ the length of the basis. The worm lives on the gills when young, migrating to the egg masses where it reaches sexual maturity.

Van Beneden (1861) gives no diagnostic information which is not better given by Coe. On Pl. III there are figures of the head region, the eggs, and the free-swimming larvae. In these the basis and stylet are not distinguished, but are drawn as one structure. The "everted proboscis" apparently is the esophagus.

McIntosh (1873-1874) has little to add. He gives figures of the whole worms (in color), on Pl. I, fig. 5; the proboscis on Pl. XII, fig. 14; the head region on Pl. XIV, fig. 4; the ovum on Pl. XVI, figs. 18, 19, and 20; and the ciliated larva and spermatozoa on Pl. XVII, figs. 7 and 9. The stylet apparatus in Pl. III, fig. 14, has the ratio of stylet to basis of 0.543.

Bürger (1895) stated that the mucous sheaths are 8-12 mm in length, and that the males and females are of different sizes, the male worms

TABLE 1.—MEASUREMENT (IN MICRONS) OF STYLET APPARATUS OF *Carcinonemertes carcinophila* (KÖLLIKER) MADE BY COE IN NEW ENGLAND

Length of Basis	Length of Stylet	S:B Ratio
25	8	0.320
19	6	0.316
22	7	0.318
30	12	0.400
23	9	0.390

being 4-5 cm and the females 3 cm in length. This is the exact reverse of the condition found by the writer in other species of the genus and in the new variety to be described below, and may possibly be a *lapsus calami* on Bürger's part.

In correspondence with the writer (November 8, 1940) Dr. Coe gave the following additional figures, shown in Table 1, regarding individuals of *Carcinonemertes carcinophila* (Kölliker) in New England which he studied.

Takakura's duct, to be described in detail below, is present in this species. In structure it is similar to that to be described in *Carcinonemertes carcinophila* var. *imminuta*.

Cephalic muscle fibers (cf. fig. 9), similar to those to be described below for the new variety, are present in the head region, especially along the sides of the rhynchodaeum.

The mucous sheath of one of the worms recovered from the egg mass of a specimen of *Ovalipes ocellatus* (Herbst) in the Museum of Com-

TABLE 2.—MEASUREMENTS OF *Carcinonemertes carcinophila* (KÖLLIKER) FROM NEW ENGLAND

Sex	Length (mm)	Diameter (mm)	Basis (μ)	Stylet (μ)	S:B Ratio	Middle Chamber (μ)	Posterior Chamber (μ)
Male...........	3.0	0.385	23 x 6.5	...	.....	32 x 28	63 x 49
Male...........	3.0	0.420	....	...	.....	30 x 27	52 x 43
Male...........	1.5	0.280	24 x 6.0	8.5	0.354	30 x 25	60 x 40
Female.........	3.0	0.420	23 x 6.0	...	.....	42 x 32	77 x 53
Male...........	2.5	0.490	....	...	.....	30 x 31	60 x 42
Male...........	3.0	0.350	24 x 6.5	8.0	0.333	32 x 28	......
Male...........	2.5	0.315	23 x 6.5	...	.....	39 x 30	65 x 45
Averages.......	2.6	0.380	23.5 x 6.3	8.3	0.344	34 x 29	63 x 48

parative Zoology is shown in fig. 11. Only a few scattered small lapilli are present.

The outline of the basis, drawn from sectioned material, is shown in fig. 27.

The measurements of the worms taken from crabs in the Museum

TABLE 3.—THE DISTRIBUTION OF *Carcinonemertes carcinophila* (KÖLLIKER)

Host	Locality and Collector	Name Given
Galatheidae		
Galathea strigosa L.......	Messina, Sicily; Dieck, 1874	*Cephalothrix galatheae*
Portunidae		
Carcinides maenas (L.)...	Ostende, Belgium; Van Beneden, 1861 and 1883	*Polia involuta*
	Roscoff, France; Joubin, 1890	*Nemertes carcinophila*
	St. Andrews, Scotland; McIntosh, 1873-1874	*Nemertes carcinophila*
	Wimereux, France; Giard, 1888 and 1890	*Nemertes carcinophila*
Callinectes sapidus R....	Beaufort, N. Carolina; Coker, 1901	"Nemertean"*
	Beaufort, N. Carolina; De Turk, in correspondence	*Carcinonemertes carcinophila*
Callinectes ornatus O....	Beaufort, N. Carolina; De Turk, in correspondence	*Carcinonemertes carcinophila**
Portunus spinimanus L..	Beaufort, N. Carolina; De Turk, in correspondence	*Carcinonemertes carcinophila**
Ovalipes ocellatus (H.)...	North Dennis, Mass., and other regions south of Cape Cod; Coe, 1902a	*Carcinonemertes carcinophila*
	Nobska Point, Katama Bay, Nememsha Bight, Woods Hole region, Mass.; Sumner, Osburn, and Cole, 1913	*Carcinonemertes carcinophila*
	Beaufort, N. Carolina; De Turk, in correspondence	*Carcinonemertes carcinophila**
	Buzzard's Bay, Mass.; M.C.Z. 5447	*Carcinonemertes carcinophila*
	Provincetown, Mass.;* M.C.Z. 5444	*Carcinonemertes carcinophila*
Ovalipes ocellatus guadulpensis (Saussure)...	Beaufort, N. Carolina; De Turk, in correspondence	*Carcinonemertes carcinophila**
Xanthidae		
Xantho floridus Mont. ...	Concarneau, France; Giard, 1888	*Polia xanthophila*
"Small crab"...........	Messina, Sicily; Kölliker, 1845	*Nemertes cartinophilos*

*These worms may be referable to the variety *imminuta* to be described below.

of Comparative Zoology (*Ovalipes ocellatus* (Herbst), M. C. Z. Nos. 5444 and 5447) are shown in Table 2. The blank spaces appear because in those instances the section was cut at such a plane that accurate measurement of the structure involved was impossible.

Geographical Distribution and Hosts

The distribution of *Carcinonemertes carcinophila carcinophila* (Kölliker) in respect to both geographical localities and hosts is indicated in Table 3.

CARCINONEMERTES CARCINOPHILA (KÖLLIKER) VAR. *IMMINUTA* VAR. NOV.

Specimens of *Carcinonemertes carcinophila* (Kölliker) were found at Grand Isle, Louisiana, and collected from crabs from various parts of the West Indies and South America, which, although they conform in most respects to the *C. carcinophila carcinophila* found in New England and Europe, nevertheless show a few morphological differences. A detailed description of these worms, constituting a new variety, *Carcinonemertes carcinophila* var. *imminuta*, taken from *Callinectes sapidus* Rathbun, at Grand Isle, Louisiana, is given below.

Morphology

Shape and Size.—Sexually mature individuals, which are found only on the egg masses of the crab, are greatly elongated, filiform, cylindrical worms, tapered bluntly at both ends. Each worm secretes around itself a closely fitting, lapilliform sheath of semi-transparent material. Within

Table 4.—Sizes (in mm) of Mature Female *C. carcinophila* var. *imminuta*

Length (extended)	Width	Number of Ovaries
0.420	0.098	8 on left, 7 on right
1.480	0.162	12 on each side
1.665	0.177	9 on left, 10 on right
7.0	0.210	44 on each side
15.0	0.220	67 on each side
20.0	0.220	130 on each side
23.0	0.240	120 on each side
25.0	0.230	145 on each side
26.0	0.240	147 on each side
27.0	0.270	100 on each side
35.0	0.300	185 on each side

the sheath the worm can move about, forward or backward, or even double upon itself. The largest mature individuals usually attach their sheaths near the bases of the endopodites and consequently are well hidden among the eggs of the crab. Younger individuals are often abundant on the periphery of the egg mass.

Sexually mature females reach greater lengths than do the males. The largest adult female seen measured 35.0 by 0.3 mm when extended and 15.0 by 0.35 mm when contracted. The smallest adult female was 0.420 by 0.098 mm, when measured under slight pressure of a cover-glass. A number of adult females were measured to obtain some idea of the average size. Their measurements are shown in Table 4. The average length of these eleven worms is 16.55 mm and the average width 0.22 mm. The averages are not exact, however, because precise measurement of the very sensitive and highly contractile bodies often makes measurement practically impossible. In general, from the writer's numerous observations on living specimens, it may be said that adult females from 10 to 30 mm in length are found much more often than individuals of other sizes. In passing, it may be noted that the number of ovaries increases with the length of the worm, an observation to which reference will be made later.

Sexually ripe males tend to be smaller, and never reach the maximum size of the females. Although the same difficulties encountered in measuring the females were present here also, the figures shown in Table 5 were recorded. These twelve males show an average length of 8.68 mm and an average width of 0.214 mm. The largest adult male observed was 16.0 by 0.27 mm and the smallest, 0.928 by 0.131 mm. The sizes most often encountered were between 5 and 15 mm in length. The testes are not arranged with regularity as are the ovaries, but are scattered in the body. Hence their number was not counted, although it is probable almost beyond any doubt that they increase in number similarly with the lengthening of the worm.

A real sexual difference in size exists in this and other species of the

TABLE 5.—SIZES (IN MM) OF MATURE MALE *C. carcinophila* VAR. *imminuta*

Length (extended)	Width	Length (extended)	Width
0.928	0.131	10.0	0.23
1.036	0.144	11.0	0.24
1.202	0.181	11.0	0.23
9.0	0.21	12.0	0.25
10.0	0.26	12.0	0.22
10.0	0.20	16.0	0.27

genus Carcinonemertes. Bürger (1904, p. 25) gave the following meas-
urements for *C. carcinophila:* length of female 40 to 50 mm, length of
male 30 mm. The same author (1897-1907, p. 420) gave for the males
30 mm and for the females 40 to 70 mm. The measurements given in
the preceding paragraphs of *C. c. imminuta* show the mature females to
be often two to three times as long as the males. It is true, of course,
that individual females can be selected which will be much shorter than
the largest males. On the other hand, the fact remains that males have
never been observed to reach as great lengths as the females. Van Bene-
den (1861, p. 20) stated that in *Polia involuta* (= *Carcinonemertes car-
cinophila*), from *Carcinides* (= *Carcinus*) *macnas* (Linnaeus) in Bel-
gium, the females are 2 to 3 cm long, while the males are only 1 cm in
length. Takakura (1910) stated that in the Japanese species *C. mitsu-
kurii* Takakura the females are 3 cm or more in length, while the males
are only 1 cm long. The situation in the Californian species *C. epialti*
Coe may be similarly dimorphic, although according to Coe (1902a) the
sexually mature individuals measure from 4 to 6 mm in length. How-
ever, *C. epialti* is a small-sized species and differences in size between the
sexes would consequently be more difficult to recognize. Perhaps future
work will disclose such differences. Coe (1920) stated that in the ne-
merteans "little evidence is available as to the size factor in relation to
sex, but in general the exceptionally large individuals are females."

There are no indications of any suckers, hooks, adhesive pads, or
clasping organs, structures which are often found in parasitic animals.
The body is smooth and of the same diameter throughout (fig. 42).

The small size at which sexual maturity is reached in some individuals
is remarkable, in that no other nemerteans are known to the writer to
become sexually mature at such minute sizes. Bürger (1897-1907, p. 35)
stated that among the Nemertea "Die kleinsten sind 3-10 mm lang und
nur den Bruchtheil eines Millimeters breit (Oerstedia)." Böhmig (1933,
p. 4) gave as the lower limit of length 5-10 mm. Coe (1905a, p. 5)
mentioned minute species of Tetrastemma but 5 mm long and 0.5 mm
thick when sexually mature. Willemoes-Suhm (1874, p. 411) in a brief
description of the nemertean which he found on the abdomen of *Planes*
(= *Nautilograpsus*) *minutus* (Linnaeus) stated that the worm did not
exceed 2 mm. However, none of the specimens examined by him had
the genital organs developed. Van Beneden (1861, p. 18) stated that
in *Polia involuta* (= *Carcinonemertes carcinophila*) "On trouve déjà
dans leur gaine, entre les oeufs de crabe, des jeunes qui n'ont pas plus
du double de leur largeur." Whether these were sexually mature indi-
viduals was not definitely stated. Friedrich (1933) found specimens of
Arenonemertes microps Friedrich which were only 2-3 mm in length

when mature. *Carcinonemertes carcinophila* var. *imminuta* reaches sexual maturity 'at the smallest sizes known for any nemertean.

Body Surface.—The entire body is ciliated (figs. 14-19). At the anterior end there is a minute funnel-like depression about 20 μ in diameter, which is the opening of the rhynchodaeum. Through this opening in the body wall the food enters the body. The sphincter-like walls around the opening are capable of great extension. In most live worms, this opening is difficult to see under ordinary powers of magnification because of the opaque, refractile quality of the surrounding parenchyma and gland cells. The anus (fig. 15, A) is situated at the posterior end of the body. This posterior opening is about the same size as that of the rhynchodaeum, and the surrounding walls are capable of extension to allow material from the alimentary canal to pass out of the body. There are no other landmarks on the body surface than the entrance to and the exit from the alimentary canal. Such organs as cephalic slits and furrows, sensory pits, and frontal sense organs are absent.

Color.—Many adjectives have been used by various authors to describe the color of *C. carcinophila*. The color of the variety *imminuta* appears to be no different from that of *carcinophila*. Coe (1902a) described the color of the latter as "yellowish, orange, pale reddish, rose-pink (McIntosh), or bright brick-red." Immature specimens of *C. c. imminuta* and those in which the gonads are not well developed are rather uniformly orange-red to flesh color. This color makes their detection on newly laid crab eggs, which are bright orange-yellow, rather difficult. As the crab eggs become older, their color darkens to a rich brown or black, and on these eggs the worms are readily visible. When an individual worm is placed on a glass slide, it appears whitish, especially if flattened under a coverglass. However, if several worms are allowed to crawl together in a finger bowl, the color of the resulting mass is a bright orange-red.

A delicate distinction in color exists in the two sexes when mature. The males are whiter and lack much of the orange-red shade. The difference in color is probably accounted for by the absence of large intestinal diverticula and by the appearance of abundant light yellowish or opaque testes. Under low power the alimentary canal appears as a straight, broad, grayish line, about one-third the diameter of the worm. Large mature females are flesh-colored to orange-red, sometimes even approaching a bright red. The large intestinal diverticula with their yellow to orange-brown walls and the abundance of eggs are probably factors in increasing the intensity of color in the female. Individuals which are flattened out under a coverslip appear similar in color in transmitted light. However, with practice, it is relatively easy to distinguish

sexes when the worms are still on the egg masses. The larger the mature worms the more pronounced the color differences seem to be. The cephalic region generally appears somewhat paler than the rest of the body because of the nearly colorless esophagus and proboscis and the absence of the gonads and intestine in that region.

Differences in color between the sexes are already well known in the Nemertea, although they have been previously unrecognized in Carcinonemertes. Riepen (1933, p. 332) described the color of *Malacobdella grossa* (Müller) as follows:

> Die Männchen sind zumeist weisslich bis grau, die Weibchen gelblich bis bräunlich gefärbt. Dadurch ist ein sicheres äusseres Unterscheidungsmerkmal der Geschlechter werden. Bei geschlechtsreifen Weibchen tritt der Unterscheid vom Männchen ausserdem dadurch hervor, dass die seitlichen Partien der hinteren Körperhälfte gegenüber dem übrigen Körper bedeutend dunkler (tief braun) gefärbt sind. Diese Erscheinung ist auf den Inhalt der Ovarialsückchen (Eier und deren mit Dottermaterialen angefüllten Nährzellen, siehe Kapitel Gonaden) zurückzuführen. Die von Spermatozoenmassen erfüllten Hodensäckchen sind von milchigweisser Farbe, so dass bei den Männchen die Gonadenregion vom übrigen Körper nicht merklich abgehoben erscheint.

In *Cerebratulus lacteus* (Leidy) and in many other species there is, as mentioned by Coe (1920), sexual dimorphism in respect to color, although this differentiation may be apparent only seasonally during the reproductive period. Coe stated that "it seems not improbable that the sexes in every species if carefully observed would likewise be recognizable by color modifications when their sexual products are ripe."

Ocelli.—There are two dark yellowish-brown ocelli located laterally just anterior to the brain. In one mature female the two ocelli were located 80 μ in front of the brain, 200 μ from the anterior end of the body, 135 μ apart, and 35 μ from the sides of the body. Under low power they appear dark brown or black and more or less irregularly shaped (figs. 20, 50, and 52). Under high dry magnification the ocelli are observed to be composed of groups of light brown granules 0.4 μ in diameter. These granules are most thickly congregated in the center of the ocellus, imparting a very dark brown, almost black, color to that region. The peripheral area of the ocellus, where the granules are more scattered, is light yellowish-brown. The ocelli are 20 to 70 μ in diameter. Often the shape is not at all regular. Sometimes the yellow-brown granules are scattered at random over parts of the head region. The ocelli may not be of the same size or shape on the two sides of a single individual. One worm taken from the gills of a crab had only a right ocellus. Another worm, a mature female from an egg mass, had two pairs of ocelli, making four in all. A second pair was located at the level of the posterior margins of the brain lobes. These were only about one-sixth as large as the anterior pair. Another worm had two extra ocelli located close together at the anterior edge of the dorsal commissure of the

brain. Coe (1902b) mentioned that the two ocelli in this genus are occasionally fragmented into four. The position of the ocelli in the body will be mentioned below in the discussion of the nervous system.

Movements.—The worms are incapable of any swimming movements and depend upon a substratum for locomotion. The thousands of cilia on the outside of the body beat in successive waves and carry the worm forward. A large amount of mucus is secreted by the dermal and submuscular glands, which aids the worm in adhering to the substratum. As the worm proceeds a glistening trail of mucus is left behind. The anterior end of the body is almost constantly performing exploring motions while the worm is moving. That part of the body is very sensitive to mechanical stimuli. The movement of the worm is a gliding motion, resembling that of Planaria and other Turbellaria. There are no strong peristaltic waves of contraction and no undulatory movements, such as are present in many nemerteans. The production of mucus is no doubt of great advantage to the worms, since it enables them to adhere to the carapace of the crab or to the endopodite hairs or eggs, withstanding the currents of water which might otherwise throw them off. The mucus also provides a suitably soft, yet resistant, substratum against which the cilia can work (Friedrich, 1932, p. 539).

When the worms are violently stimulated, by pinching, lack of water, acids and other strong chemicals, etc., they may contract the musculature of the body wall, throwing themselves into variously coiled masses. Strong peristaltic movements may occur under such stimulation. In the normal, unstimulated worm, gentle waves of contractions pass along the body, aiding indirectly the movement of food materials in the alimentary canal.

Adult worms of both sexes are negatively phototactic. When infested egg masses are placed in a finger bowl of clean sea water, many of the worms leave their mucous sheaths and crawl to the side of the dish away from the source of light. Worms on the gills of the crab seem to be even more strongly negative in their reaction to light. When infested gills are placed in a finger bowl of sea water, within a few minutes the worms break through their delicate capsule walls (text fig. 1, M) and crawl quickly to the darkest part of the dish. There they pile up on one another in an orange-red mass. When the dish is then turned 180 degrees a mass streaming of the worms across the bottom of the dish back to the opposite side away from the source of light occurs. Such negative phototaxis is not rare in the Nemertea. In fact, according to Böhmig (1933, p. 60), all adult nemerteans behave thus, except perhaps *Oerstedia dorsalis* (Abildgaard), which according to the observations of von Buddenbrock (1923, p. 1) is positively phototactic. The free-swimming young forms of *C. c. imminuta* are positively phototactic, a phenomenon which will be

mentioned below in the discussion of the life history. When heavily infested egg masses are placed in a finger bowl of clean sea water, the water on the side nearest the source of light becomes cloudy with free-swimming larvae within a few hours. The smallest crawling worms observed were weakly negative to light, but those from about one
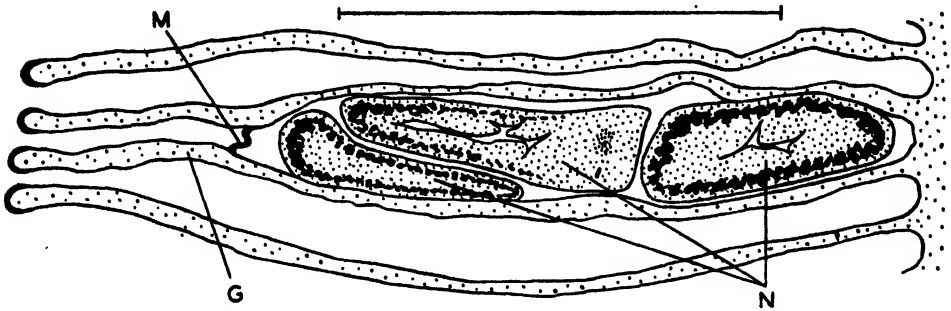
TEXT FIG. 1.—Longitudinal section of infested gill of *Callinectes sapidus*, showing capsule and coiled nemertean. Stained with Delafield's haematoxylin and eosin. Scale 1 mm. *M*, mucous wall of capsule secreted by nemertean; *G*, gill lamella; *N*, body of nemertean.
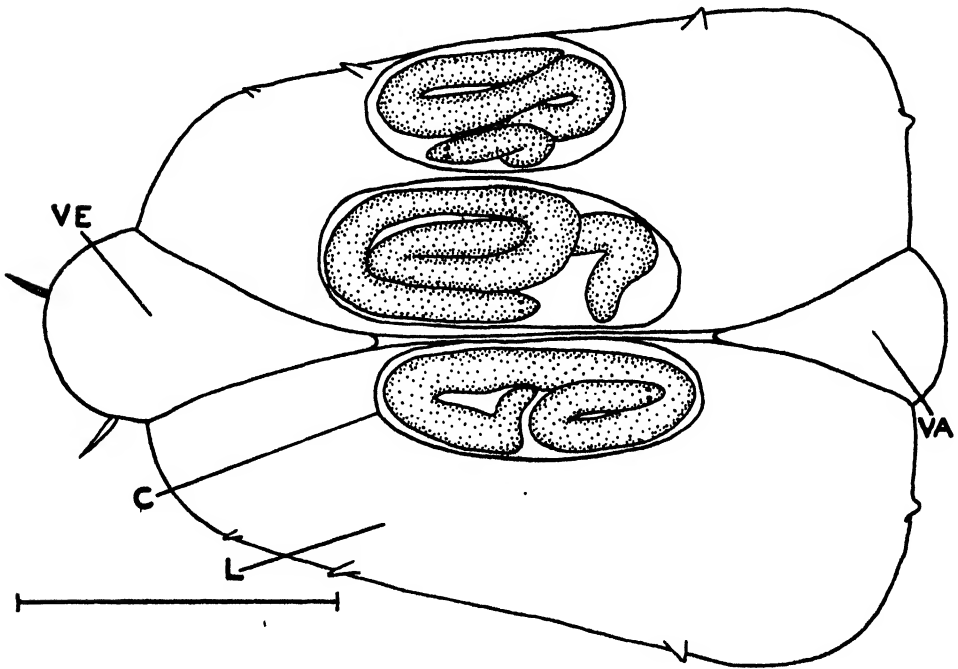
TEXT FIG. 2.—End view of gill lamella of *Callinectes sapidus* showing position of worm capsules. Scale 2 mm. *VA*, afferent blood vessel; *C*, capsule of nemertean; *L*, lamella of gill; *VE*, efferent blood vessel.

millimeter in length showed definite negative phototaxis. There is, then, a reversal in response to light occurring probably at the time when the free-swimming larva settles down to a crawling existence. Such a reversal of response has been observed by Reisinger (1926, p. 9) in the fresh-water nemertean *Prostoma graecense* Böhmig.

Location on Host Crab.—Sexually mature worms were found only on the egg masses of the crabs, although worms in which rudiments of ovaries could be distinguished were found occasionally on the gills. In one of these there were eight pairs of ovaries, each about 40 μ in diameter and composed of several large, granular, whitish cells. Each rudimentary ovary was situated in a slight invagination of the intestinal wall. Most of the worms on the gills, however, show no indication of gonads when observed under low power *in vivo*. All the worms on the gills live irregularly coiled in capsules between the gill lamellae (text fig. 2). A wall of what is apparently hardened mucus (text fig. 1, M) secreted by the worm cements the two lamellae together, closing off free communication between the worm in its capsule and the surrounding sea water. Only one worm occupies each capsule. As many as six such capsules have been observed between two gill lamellae. Heavily infested gills may harbor several hundred worms.

Sexually ripe males and females, as well as those nearly mature and those which have recently spent their sex products, are found scattered on the egg masses of the crab. The adults most often occur concealed among the eggs, however. The mucous sheaths in which they live are usually attached near the bases of the endopodites. Occasionally mature worms of small size are found on the periphery of the egg mass, but here immature worms or worms in which the gonads are just beginning to form are more common.

Mucous Sheaths.—The mucous sheaths, in which the adult worms live, are apparently of the same structure in the two sexes. The proximal end of the case is fastened to the endopodite hair of the crab. The exact point of attachment is indistinguishable. The mucous material of the sheath is continuous with the material which covers the endopodite hairs. The middle region and distal end of the case are unattached. One of the largest sheaths seen, that of an adult female, measured 25 mm in length. The sheaths are elastic and can be stretched to two or three times their original lengths. The surface of the sheath is lapilliform, that is, covered more or less completely with small, irregularly shaped, raised concretions (figs. 7, 12, 13, and 32). These are largest in the middle region of the sheath (fig. 13) and decrease in size toward both ends, finally disappearing entirely (figs. 7 and 12). As they diminish in size they tend to be more angular and become more numerous. There is no regular pattern in their arrangement and even in the middle region of the sheath, where

most of the concretions are large, a few smaller ones may be found among them. When viewed under high power the raised areas show concentric striae resembling growth lines. The walls of the sheaths are thin and transparent, and, except in the central lapilliform region, are collapsible. When the worm withdraws, the walls wrinkle and come together. Possibly the concretions of the mucus-like substance of the middle region serve to prevent the collapse of the sheath and thus to offset the consequent pressure on the body of the worm.

Although the sheaths vary in length, they are always longer than the worm in its contracted state. The sheath of a very small adult female, 1.665 by 0.177 mm, (fig. 32) showed none of the prominent raised lapilli, but faint markings on the surface may indicate their future positions. The promixal part of the sheath showed coarse, irregular granulations. There were several longitudinal folds in the central region, probably caused by the collapse of the walls, when the worm retreated from the sheath.

At the time of egg laying, part of the sheath becomes a container of the eggs (fig. 21). As will be mentioned again, the female deposits eggs which adhere all about her to the wall of the sheath. She then retreats from the scene, the elastic walls of the sheath contract and the result is a tube filled with eggs. The female sometimes forms one or several branches to the main sheath, in which she deposits her eggs. She may, however, simply lay her eggs in an extension of her own sheath. The wall of that part of the sheath which encloses the eggs never bears the lapilli found on the main section of the sheath, probably because the temporary nature of the egg sheath does not allow time for the formation of such lapilli. The sheaths of male worms occasionally show side-branches, although certainly these are not used for egg-laying. The egg sheaths sometimes contain enormous numbers of eggs. One such sheath 10 mm in length was estimated to hold 1200 eggs.

Sexually mature worms of both sexes, as well as those showing no evidence of gonads *in vivo* and those which had already given off their sex products, were found living in sheaths. In fact, no sexually mature worms were seen outside the sheaths, except hours after the capture of the crab, when the worms had been irritated by abnormal stimuli. Only one worm was seen in a sheath at one time. Van Beneden (1861, p. 20) stated that in *Polia involuta* (= *C. carcinophila*) he often found "des individus des deux sexes logés dans la même gaine." It seems beyond doubt to the writer that the two sexes must at times be together in the same sheath to bring about insemination. Otherwise the spermatozoa, which are limited in number as compared with the huge numbers present in some of the larger free-living nemerteans, would be so scattered that the majority of them would never come in contact with a female worm.

Probably the mucous sheath aids in bringing about the entrance of the spermatozoa into the ovarian ducts by confining the former until they make contact with the female. In passing, it should be mentioned that among the preserved specimens of the new species from Zanzibar to be described below there was one mucous sheath which contained both a male and a female worm.

When sectioned and stained with haematoxylin the lapilli on the sheaths stain more lightly than the thin wall of the sheath upon which they are situated (fig. 6). A cross section of a lapillus shows distinct longitudinal striae (fig. 6) in the inner half, while the outer half is opaque and granular. The outer half furthermore is stained only lightly, while the inner half becomes a light purplish blue, in contrast to the dark purplish blue color assumed by the sheath wall. The largest lapilli are about 30 μ thick. The walls of the sheath, however, measure only about 5 μ in thickness.

Body Wall.—The entire body is covered with a single layer of glandular and ciliated cells (figs. 14 to 19). In four living worms the height of these cells was 10, 9, 11, and 13 μ respectively, averaging about 10-11 μ. On the anterior end of the body the layer is thicker, measuring 22 μ in height. In fixed and stained material the epithelium measures 10 μ in thickness. Each ciliated cell contains distally a group of 8 to 12 minute granules which stain deeply with neutral red (10 drops of dilute neutral red solution in a finger bowl of sea water left overnight). In the middle region of the cell there is a slightly elliptical nucleus lying parallel to the long axis of the cell. When viewed in any one optical plane approximately six cilia can be seen along the distal margin of the cell. These average 4.5 μ in length over most of the body, but are 6 μ long on the anterior end. The ciliated cells on the anterior end of the body are not only taller but also relatively more slender than the cells covering the rest of the body. Gland cells are fewer in number. In a worm whose epithelium has been stained with neutral red the large gland cells filled with a reddish stained secretion can be seen clearly under oil immersion. They are more numerous in the head region and hence that region stains more deeply with neutral red.

Immediately below the outer layer of cells there is a thin basement membrane 0.5 μ thick. Because of its extreme thinness and hyaline nature this structure is hardly distinguishable in life even under high magnification. In sectioned material stained with fast green or with Delafield's haematoxylin the membrane is colored strongly, appearing as a fine line extending around the body just below the epithelial cells of the integument.

Internal to the basement membrane there is an extremely thin layer of circular muscles. The entire layer is not over 1.5 μ thick in sectioned

worms. In living animals the fibers are extremely difficult to make out in any detail. Each fiber seen in fixed and stained material is about 1 μ or less in diameter. In longitudinal sections the fibers can be seen as faintly stained lines superimposed upon the relatively massive longitudinal fibers. The weak development of the circular muscle fibers probably accounts both for the absence of strong peristalsis and for the inability of these worms to fragment the body. At the opening of the rhynchodaeum and at the anus the circular fibers no doubt act as sphincter muscles (fig. 15, CM).

A layer of longitudinal fibers is situated immédiately below the circular layer. Like the latter this layer forms a continuous muscle tube around the body. In life the individual fibers are not distinctly visible, but in sectioned and stained specimens they show prominently, especially when Delafield's or Heidenhain's haematoxylins are used. The longitudinal layer as seen in the extended living worm is usually 2 to 3 times (3-5 μ) as thick as the circular layer. The relative thickness of the two layers varies greatly with the state of contraction of the body. In some sectioned specimens, which were highly contracted when fixed, the longitudinal layer is as much as 10 to 15 times (15-22 μ) as thick as the circular layer (figs. 17 and 19, LM). In life the longitudinal layer is marked with fine longitudinal, refractile lines—the edges of the individual muscle fibers. The fibers seen in sections show no nuclei and no cross striations, and their substance appears to be homogeneous. Each fiber is greatly elongated, measuring 1.5 μ in diameter and reaching sometimes more than 100 μ in length. Nuclei if present must be very minute. Coe (1905a, p. 14), while discussing the musculature of the Nemertea, stated that "Each muscle fiber consists of a single cell, with an extremely small, slender nucleus, surrounded by an insignificant amount of undifferentiated cytoplasm. This minute cell body lies upon, or imbedded in, the fiber of contractile substance." Between the loosely arranged fibers the necks of the submuscular glands extend outward to the integumental epithelium.

Anteriorly to the level of the brain the longitudinal muscle layer decreases in thickness. The fibers bend inward, passing among the cephalic glands and parenchymal cells (cf. fig. 9). Many of the fibers extend transversely, others obliquely. Along the rhynchodaeum, where the majority of these fibers are located (fig. 16), there are longitudinal fibers also. In living worms under high magnification, twitches in the region surrounding the rhynchodaeum and changes in the diameter of the latter are often seen. Such movements are accomplished by the contraction and relaxation of the cephalic muscle fibers. When the esophagus is everted, as will be described later, these fibers no doubt aid in increasing the diameter of the rhynchodaeum. They may also aid in forcing out

the contents of the cephalic glands. A few scattered fibers may be seen in sections of the area around the brain, the anterior part of the esophagus, and the proboscis, although none of the fibers are connected to the latter. These are probably the fibers described by McIntosh (1873-1874, Pl. XIV, fig. 4, f) as "powerful transverse fibres which retain the posterior part of the oesophagus *in situ.*" Regarding the cephalic muscles of nemerteans, Coe (1905a, p. 12) stated: "In the cephalic region of the Heteronemertea and many of the Palaeonemertea, the arrangement of the muscular layers is broken up to form a complex network of fibers running in all possible directions, but of which the longitudinal fibers are the most numerous. In other forms the two muscular layers extend forward into the head." Cephalic muscle fibers have not been previously described in Carcinonemertes.

Anterior to the brain the head is almost completely filled with clusters of cephalic glands (fig. 16, CG), which open to the outside by numerous ducts over the surface of the head. The cephalic muscle fibers pass through the masses of gland cells, and possibly aid in expelling the secretions of the glands by their contractions. Laterally to the brain lobes the cephalic glands merge gradually with the submuscular glands. In haematoxylin or safranin stained sections the cephalic glands do not become colored as deeply as the submuscular glands, and consequently they are sometimes more difficult to identify. The cell outlines are not as distinct as those of the submuscular glands. However, in sections fixed in Schaudinn's fluid and stained with methylene blue and eosin, the gland cells of both cephalic and submuscular regions become stained bright blue against a pink background.

Immediately beneath the longitudinal muscle layer there is situated a massively developed layer of gland cells, the submuscular or hypodermal glands. The contents of these glands stain heavily with safranin and with Delafield's haematoxylin. For this reason they are conspicuous in sections even under low power magnification. The layer is as thick as or thicker than the outer layers of the body wall combined. Measuring from the exterior of the body to the inner ends of the gland cells gives a distance of 50 to 70 μ. The gland cells are not simple, but several are grouped together, with their ducts converging, in a common duct to the exterior. Commonly four or five such cells empty by a common duct. The ducts pass among the muscle fibers, through the basement membrane, and among the cells of the integumental epithelium, to discharge their glandular secretion to the outside of the body. The gland cell nuclei (fig. 40, S), about 1 μ in diameter, are located in the proximal half of the cells, below the muscle layers. In life the contents of the gland cells stain red with neutral red and are coarsely granular and refractile. In fixed,

sectioned, and stained material the secretion appears finely granular and deeply stained.

Most nemerteans do not have such a remarkable development of the submuscular glands. According to Coe (1905a, p. 18) these glands are usually found only in the head region or occasionally in the region of the esophagus, as in *Amphiporus nebulosus* Coe, or reaching to the anterior end of the intestine, as in *Emplectonema bürgeri* Coe. Bürger (1897-1907, p. 67) stated that "Nur bei den Eupolien werden sie im Allgemeinen recht ansehnlich an Länge und Umfang. Hier erstrecken sie sich in die Vorderdarmregion hinein." The great extent and size of the submuscular gland layer was given by Coe (1902b) as a generic character of Carcinonemertes.

Connective Tissue and Parenchyma.—Delicate strands of connective tissue can occasionally be seen in sections among the necks of the submuscular glands, immediately internal to the longitudinal muscle layer, and among the muscle fibers. The parenchyma is greatly reduced. The intestine fills practically all the space internal to the submuscular glands (fig. 19). A few minute nuclei are scattered along the edge of the intestine, and from these the gonads probably eventually develop. Such a process has been described by Coe (1905a, pp. 64-65) for nemerteans in general. In the cephalic region anterior to the brain the parenchyma is most abundant. It fills all the space between the rhynchodaeum and the muscle layers of the body wall which is not occupied by the rhynchodaeum, muscle fibers, gland cells, nerves, or ocelli. The scarcity of parenchymal tissues in *C. carcinophila imminuta* makes a decided contrast with species like *Amphiporus gelatinosus* Coe, in which the parenchyma is several times thicker than the body wall.

Alimentary Canal.—The rhynchodaeum (fig. 16, RH) is a straight, slender tube, extending from the opening on the anterior end of the body to the region close in front of the brain, where it gives off ventrally the esophagus and dorsally the proboscis. Its lumen is about 7 μ in diameter and its wall 3.5 μ in thickness, making a total diameter of about 14 μ. It is embedded in the parenchyma of the head and surrounded by the very loose network of longitudinal, transverse, and oblique cephalic muscle fibers. The non-glandular wall of the rhynchodaeum is composed of a single layer of small, columnar, ciliated cells.

The esophagus (fig. 16, AE and PE) leaves the ventral wall of the rhynchodaeum a short distance anterior to the brain in the mid-line of the body. The anterior part, extending from the rhynchodaeum under the ventral nerve commissure to a region just posterior to the rear margin of the brain, has about the same diameter as the rhynchodaeum. As it passes posteriorly it increases gradually in diameter to about 80 μ, and its walls become folded longitudinally. In life this part of the esophagus

(fig. 16, AE) is opaque and granular, with longitudinal refractile lines caused by the folding of the wall. Both ciliated and glandular cells are to be found in its wall. The posterior end of this section of the esophagus fits like a cap on the anterior end of the thick-walled, muscular posterior part (fig. 16, PE). The junction between the two histologically very different parts is well demarcated, and located usually at about the level of the stylet (fig. 16). In a relaxed, actively crawling worm the posterior part of the esophagus lies entirely posterior to the brain. Its general shape is dolioform, with the anterior end squarely truncate where it joins the slender anterior part, and with the posterior end tapering somewhat abruptly before joining the intestine. The posterior sections of the esophagi of ten adult worms measured 85 by 50, 90 by 65, 127 by 117, 147 by 120, 150 by 80, 162 by 95, 190 by 85, 200 by 147, 252 by 140, and 378 by 41 μ respectively. The esophagus is always longer than its diameter. The ten measurements gave an average length of 178 μ and an average diameter of 97 μ.

The posterior part of the esophagus in the live worm is very conspicuous both by its whitish color and by the anterior and posterior contractions of its body wall. The ciliated and glandular epithelial lining is surrounded externally by a layer of distinct circular muscle fibers, which in their shape, size, and staining resemble those of the body wall and head. Occasionally a few longitudinal muscle fibers may be seen external to the circular layer. These are more weakly developed however. The entire wall measures 17 μ in thickness, leaving a spacious lumen of about 150 μ in diameter.

In contracted worms under pressure of the coverglass the esophagus may be moved forward so that it lies almost wholly anterior to the brain (figs. 50 and 52). In three worms the esophagus was observed to move anteriorly until the thin anterior part was everted outside the body (fig. 52, AE) and the muscular posterior part (fig. 52, PE), its circular muscles contracting spasmodically, reached nearly to the inner edge of the integumental epithelium. Partial eversion of the esophagus was sometimes seen in worms placed in sea water on a slide with no coverglass. In two worms under pressure the anterior part was completely everted, so that the posterior part was brought completely outside the body. The latter continually underwent convulsive peristaltic contractions of the circular muscle fibers, beginning at the anterior end and progressing rapidly posteriorly. In both cases the worms kept the esophagus everted for only a few seconds, so that a camera lucida drawing was impossible. However, sketches of one of the worms were made (fig. 51, A, B, and C). The arrow shows the direction of peristaltic contractions. Both worms were able to withdraw their esophagi and apparently were uninjured by the experience. When the esophagus is thus everted the proboscis is at the

same time drawn far anterior to its normal position behind the brain. However, the esophagus is responsible for the movement of the proboscis. The latter is entirely passive, showing no contractions of any of its parts which might alter its position in the body.

Van Beneden (1861, Pl. III, fig. 5) published a drawing of the anterior end of the head of *Polia involuta* (= *C. carcinophila*) in which the esophagus, and not the "proboscis" as Van Beneden interpreted it, is everted. The thick walls and the ciliated interior of the everted part both indicate that it is the posterior muscular part of the esophagus and not the proboscis which is everted. At the distal end of the everted structure Van Beneden represented three curved, spine-like objects, unmentioned in the text of his paper. These may have been bunches of cilia. Certainly they are not stylets, since this species has only one. The writer suspects that this figure was drawn very hastily, since the worms do not keep their esophagi everted for more than a few seconds, and then perhaps copied later from sketches or from memory.

The posterior end of the esophagus is surrounded by the anterior end of the intestine, into which it empties directly. The intestine extends in the middle region of the body posteriorly to the anus. As already mentioned, the yellow-orange to brown color of the intestinal walls contributes greatly to the general color of the worm. In sexually mature females the intestine is deeply lobed on both sides of the body (fig. 34), probably because of the pressure of the alternating ovaries. In young worms or those in which the ovaries are undeveloped, there is only a very slight and somewhat irregular crenation of the intestinal wall. In adult males the wall is likewise nearly straight, since the irregular disposition of the numerous testes does not create local pressures on the intestine to force the wall into pouches. The walls of the intestine are, however, slightly scalloped to fit the contours of the contiguous testes. The shape of the intestinal pouches varies with the size of the ovaries and the state of contraction of the worm. When the worm is contracted the pouches are located usually directly opposite one another, but when extended the pouches alternate in a zigzag course. The number of pouches varies with the size and age of the individual (Table 4). The smallest number of pouches observed was 15 (8 on the left and 7 on the right) in an adult female 0.420 by 0.098 mm. The largest number found was 370 (185 on each side) in an adult female 35.0 by 0.3 mm. The anterior end of the intestine in large females usually lacks pouches for a distance of about 1 mm, the ovaries being absent there. The first few anterior pouches are small, but increase in size as the ovaries increase. Thereafter, both pouches and ovaries are approximately the same size until the posterior part of the body is reached. There the last few pouches diminish in size

with the dwindling ovaries, and, when the intestine passes posteriorly to the blood vessel and nerve commissures, its border is straight.

The intestine contains a great number of clear globules (fig. 47) 4-12 μ in diameter, which are suspended in a fluid substance. In addition there are often numerous dark brown or black particles of irregular or oval shapes. These measure from very small sizes up to 25 μ in length. Some of the chromatophores in the crab embryos are of similar size and shape. The fact that these particles were found only in worms removed from brown egg masses, in which the crab embryos are well pigmented, and never in worms taken from the gills, together with the additional evidence that they were absent in worms from yellow-orange egg masses, in which the crab embryos are as yet unpigmented, leads the writer to the conclusion that these nemerteans are able to feed upon the crab eggs. The mechanism of this is unknown since the process has never been observed in the laboratory. It is possible that the sucking action of the powerful muscular esophagus can break the egg membrane by continued pulling and then draw out the soft embryo within. Parts of crab embryos were seen in the intestine of a nemertean from *Callinectes marginatus* (Milne-Edwards), to be described below. The walls of the intestine have no contractility of their own and contain no muscle fibers. However, when the body wall contracts, the contents of the intestine are moved violently back and forth.

The intestinal wall (figs. 14, 15, 16, 18, 19, and 40, I) consists of a single layer of tall, columnar cells which probably are sparsely ciliated, although this detail could not be ascertained from the material available to the writer. Coe (1905a, p. 22) stated that in the nemerteans "these cells are actually provided each with a few very long cilia of such delicacy that they are seldom distinguishable in prepared sections, although they are readily demonstrated in life." Each cell contains a nucleus in its central region and numerous small granules which stain deeply with safranin or Delafield's haematoxylin scattered through the cytoplasm.

The intestine opens at the posterior end of the body (figs. 15 and 20, A) at the base of a terminal, funnel-like depression. The anus has no definite limits, but is a simple tube about 5 μ in diameter in sectioned material, capable of some distension in life,· which passes through the layers of the body wall to allow the discharge of materials from the intestine. In the region of the anus the musculature of the body wall disappears and the integumental epithelium becomes continuous with the intestinal epithelium. The circular muscle layer of the body wall forms a sphincter muscle around the anus, controlling its opening and closing (fig. 15, CM).

Proboscis.—The proboscis, situated dorsally and somewhat laterally

to the esophagus (figs. 16 and 20, AC, MC, and PC), is very much reduced in size, reaching posteriorly scarcely beyond the posterior end of the esophagus. It is divided into three chambers, anterior, middle, and posterior, the cavities of which are continuous. The anterior chamber (fig. 16, AC) extends only to the level of the posterior limits of the brain, in decided contrast to most Hoplonemertea in which the anterior chamber constitutes by far the major part of the proboscis and the stylet apparatus is located far posteriorly in the body. In *C. c. imminuta* the stylet apparatus (fig. 16, BA) is located at the level of the muscular part of the esophagus. The round middle chamber (fig. 16, MC) and the elongated posterior chamber (fig. 16, PC) follow. The length of the proboscis varies in different specimens, but it usually extends to the anterior end of the intestine, a distance of approximately 0.42 mm from its point of origin in the dorsal wall of the rhynchodaeum. The shape of the proboscis depends on the state of contraction of the worm. In a relaxed worm the proboscis may be ten times longer than its diameter, but in a contracted specimen, only four times its diameter.

The proboscis sheath is very much reduced. According to Coe (1902a) the sheath of *C. epialti* Coe "consists merely of a few fibers of connective tissue, supporting a very thin, flattened epithelium, and can be seen only in favorable preparations." In *C. c. imminuta* no trace of the proboscis sheath could be seen in life, and in sections only a few delicate strands of connective tissue, probably belonging to the sheath, can be seen at the junction of the middle and posterior chambers. These strands may be only parts of parenchymal cells however. The muscles attached to the proboscis in many nemerteans are entirely absent here. The proboscis is embedded directly in the surrounding parenchyma. During the writer's observations the proboscis was never seen to move, except for very slight changes in shape of the muscular middle chamber. The whole proboscis may be pulled about in position, as described above, by the movements of the esophagus. Even when the worms were subjected to stimuli which would readily cause large, free-living species to throw out their proboscides, there was no movement of the proboscis in this species. The worms were stimulated sometimes to the point of death by heat, dilute HCl, glycerine, alcohol, fresh water, and mechanical pressure, all without eversion occurring. It is believed by Coe (1905a, p. 27) that in Carcinonemertes "the single stylet . . . . can be everted only as far as the opening of the rhynchodaeum. . . . . With the rhynchodaeum opening pressed against the tissues of the gills of the crab on which this nemertean lives the stylet can thus puncture the gills. The exuding blood and other fluids are then drawn into the nemertean's stomach where they serve as food." The worms from Grand Isle have never been seen by the writer to evert the anterior chamber of the

proboscis, which would be mechanically necessary to bring the stylet to the exterior of the body. In his description of *C. epialti,* Coe (1902a) wrote:

The stylet can hardly be moved much beyond the external opening of the rhynchodaeum, and from a study of its structure alone it is hard to conceive how it can be moved for even this short distance, imbedded as it is among the other tissues. By crushing and many kinds of stimuli I have seldom been able to cause the worms to move the stylet region to any extent either forward or backward. It nearly always remained in the vicinity of the brain. It is my opinion that the proboscis can be everted only far enough to bring the stylet a little beyond the opening of the rhynchodaeum on the tip of the snout, as figured by Van Beneden (1861), and that esophageal muscles aid in this movement. At the tip of the snout the stylet can puncture the tissues and blood vessels of the crab's gills. With the rhynchodaeum of the worm widely opened and closely applied to the point of puncture, the blood and nutritive fluids exuding from the wound can be drawn directly into the rhynchodaeum and thence into the esophagus by the contraction of the muscular walls of the latter.

Coe evidently accepted Van Beneden's drawing of what is apparently the esophagus as that of the proboscis. The writer is forced to conclude that the proboscis is incapable of eversion, and that the stylet is not used for puncturing the gills.

The anterior chamber of the proboscis (fig. 16, AC) extends from its point of origin in the dorsal wall of the rhynchodaeum immediately on front of the brain through the brain ring, formed by the ganglia with their dorsal and ventral commissures, and ends a short distance behind the brain. Its anterior end is narrow, about 10 μ in diameter in extended worms. The posterior part gradually widens to about 50 μ. The wall of the chamber consists of a thin flattened epithelium. No muscle fibers could be seen in the sections. The highly glandular epithelium so common in many of the Nemertea is absent. The lumen of the chamber is somewhat triangular, with the stylet apparatus protruding into it at the posterior base of the triangle.

The anterior chamber is connected with the middle chamber by a narrow canal 35-40 μ in length, whose lumen measures 7.5 μ in diameter. Immediately dorsal to this connecting duct there is located a thick glandular enlargement in which the basis and stylet are embedded (fig. 16, GL). The walls of the enlargement, about 20 μ in greatest thickness and 40-50 μ in length, surround the basis and stylet laterally but not anteriorly and posteriorly. Ventrally and dorsally to the basis the walls are very weakly developed. They are composed of a single layer of large, columnar, glandular cells, whose nuclei are situated in the distal half of the cells. In life the epithelium is opaque and yellowish, with many granules. It stains readily with neutral red, becoming a light red in color. In sections these cells stain easily with haematoxylin. These gland cells, according to Coe (1905a, pp. 36-37), empty into the anterior proboscis chamber in most Hoplonemertea. Enclosed within these glandular walls

there is an oval, clear area (figs. 16 and 36), measuring 29 by 13 μ, in which the basis and stylet are located. In life the substance in this area is hyaline with no visible structure. However, in sections treated with Heidenhain's iron haematoxylin or Feulgen's nucleal reaction, there can be seen a single layer of small cells surrounding the basis, forming as Coe (1905a, p. 36) suggested "a mold into which their secretions are poured. These secretions harden and form a basis of the exact size and shape of the mold."

The basis is cylindrical (figs. 16, 20, and 52, BA; figs. 36 and 43), though not always of exactly the same diameter throughout. Both ends are bluntly rounded. On the anterior end there is a single stylet (fig. 20, S). In life the basis is granular and refractile with a yellowish tinge. It has great affinity for orange G when stained intravitally. In sectioned material the basis stains brilliant red with safranin, very dark purple with Delafield's haematoxylin, black with Heidenhain's iron haematoxylin, and light pinkish yellow with Feulgen's nucleal reaction.

The stylet is about 2/5 to 1/3 as long as the basis and acutely pointed anteriorly (figs. 36 and 43; fig. 20, S). In life it is hyaline, and no inner structure can be seen. In the living worm it remains unstained by orange G, Bismarck brown, Nile blue sulphate, neutral red, methyl green, or brilliant cresyl blue. Neither is it stained in sections with safranin, either of the two haematoxylins mentioned, eosin, or fast green. The writer is therefore of the opinion that the stylet consists of a non-living concretion of some kind of mineral matter, perhaps a calcium compound, since it is difficult to find in sectioned worms, most of which at some time in the process of preparation have been subjected to acids. In those sections untouched by acids, i.e., stained with safranin and fast green, the stylet is often visible. The junction of the stylet and basis is often irregularly defined and sometimes almost impossible to locate with precision. A slight constriction occurs in the stylet just anterior to its basal origin. However, measurements were made from the beginning of the hyaline stylet material, not from the constriction. The stylet is 3.5-4 μ in diameter at its base, but the length is variable. The lengths and diameters of bases and lengths of stylets of worms taken from crab gills, and hence not sexually ripe, and of mature worms of both sexes are shown in Table 6. The total average measurements for the 40 worms given above are: length of basis 21.0 μ; diameter of basis 5.3 μ; length of stylet 7.3 μ; stylet: basis ratio 0.347. There are no significant differences in size of the stylet and basis between the two groups of measurements. Many of the worms found on the gills probably had been sexually mature at least once before taking up their abode on the gills, and hence they should be expected to have measurements similar to those of sexually ripe individuals from the egg masses of the crab.

When the measurements of *C. c. imminuta* in Table 6 are compared with those of *C. c. carcinophila* given in Table 1, there are seen differences in size, if not in proportions. The measurements of the two sets tend to overlap somewhat, but the sizes of the stylet and basis in *imminuta* hardly reach even the average sizes of *carcinophila*. *C. c. carcinophila* from New England ranges from 19 to 30 μ for the length of the basis, 6 to 12 μ for the stylet length, the ratio of stylet to basis being 0.316 to 0.400. *C. c. imminuta* from Grand Isle, Louisiana, ranges from 19 to 23 μ for basis length, 6 to 9.5 μ for stylet length, the S:B ratio being 0.272 to 0.461. The diameter of the basis in New England worms was given by Coe (1902a) as 6 to 8 μ. In the Louisiana worms it is only 4.5 to 6 μ.

The small, round or oval middle chamber (figs. 16 and 20, MC) lies immediately posteriorly to the glandular enlargement around the basis.

TABLE 6.—MEASUREMENTS (IN MICRONS) OF STYLET APPARATUS OF *C. c. imminuta* IN WORMS FROM GILLS (NOT SEXUALLY RIPE) AND MATURE WORMS OF BOTH SEXES

Worms from Gills				Mature Worms			
Basis		Stylet Length	Ratio S:B	Basis		Stylet Length	Ratio S:B
Length	Diameter			Length	Diameter		
19.0	...	8.5	0.447	20.0	5.5	6.5	0.325
22.0	...	8.4	0.382	20.0	5.5	6.5	0.325
21.0	...	6.5	0.309	19.0	...	7.5	0.394
19.0	...	6.0	0.316	19.5	4.5	6.5	0.333
22.0	5.0	7.0	0.318	22.0	...	7.0	0.318
22.0	5.5	7.5	0.341	23.0	5.5	7.5	0.326
22.0	5.0	6.5	0.295	21.0	5.0	7.0	0.333
20.0	4.5	6.0	0.300	23.0	5.5	8.0	0.348
21.0	4.5	6.5	0.309	23.0	...	7.5	0.326
20.0	5.5	8.0	0.400	22.0	. .	6.0	0.272
22.0	5.0	6.0	0.272	22.0	6.0	6.0	0.272
20.0	5.5	7.0	0.350	19.5	5.5	9.0	0.461
22.5	5.5	9.5	0.422	20.5	5.5	7.0	0.366
22.0	5.5	6.5	0.295	21.0	5.5	8.0	0.381
20.0	5.0	8.3	0.415	20.5	5.5	6.5	0.347
22.5	5.5	7.5	0.333	21.5	5.5	7.0	0.325
20.5	5.5	7.5	0.366	19.5	5.0	6.5	0.333
22.5	5.5	7.5	0.333	20.0	5.0	8.0	0.400
21.0	5.5	8.0	0.381				
21.0	5.5	8.0	0.381				
21.5	5.5	8.5	0.395				
21.5	5.5	8.5	0.395				
21.1	5.3	7.4	0.352	20.9	5.3	7.1	0.342

Its lumen is connected with that of the anterior chamber by the above mentioned canal, and to that of the posterior chamber by a much shorter duct about 6 μ in diameter. In some worms the chamber tapers slightly anteriorly, and its anterior wall is distinctly thinner than the posterior wall. Usually it is almost perfectly round with walls of even thickness. The diameter varies in adult worms from 20 to 50 μ, with an average in 16 worms of 35 μ. The wall of the chamber, between 4 and 5 μ in thickness, is composed of a layer of longitudinal or slightly oblique muscle fibers, covered externally with a thin layer of circular fibers, and lined with a very thin flattened epithelium. In living worms the chamber is easily recognizable by its whitish color and striae (the outlines of the muscle fibers). The spacious lumen contains small, hyaline, and light brown granules suspended in a fluid material.

The third and last chamber of the proboscis is highly variable in size and shape in different individuals (figs. 16 and 20, PC). The wall of the chamber is non-muscular, and such changes as occur in its shape in the same individual are no doubt caused by contractions of the body wall and by movements of the muscular part of the esophagus, which is close by. A series of 16 adult worms of both sexes showed posterior chambers of the following sizes: smallest 34 by 34 μ, largest 336 by 84 μ, with an average size of 139 by 47.5 μ. The shape varied from round (34 by 34 μ in an adult male worm 1.2 mm in length) to greatly elongate (252 by 19 μ or about 13 times longer than its diameter in an adult female about 15 mm long). In live worms the shape varies somewhat with the pressure of the cover glass. In relaxed worms under little pressure the chamber is usually elongate, reaching posteriorly to, or in some cases even as much as 100 μ beyond, the anterior end of the intestine. In contracted worms under pressure the chamber occasionally is bent at an angle to the main longitudinal axis of the proboscis, although normally it lies in a line with the anterior and middle chambers.

The walls are thick and glandular, consisting of a single layer of irregular columnar cells, which contain large amounts of secretion readily stainable by haematoxylins. The thickness of the wall varies from 5 to 16 μ. The lumen contains minute granules 3 to 4 μ in diameter, some of which appear to stain with neutral red. The product of these glands is evidently different from the secretion of the submuscular and cephalic glands, .for, while the latter types stain brilliantly with methylene blue, the secretion of the gland cells of the posterior proboscis chamber, and indeed also that of the glands associated with the basis, stains only a faint blue. Coe (1902a) thought it probable that the substance found in the middle chamber has its origin in the posterior chamber, a supposition supported by the writer's observations.

Blood Vessels.—There are two lateral blood vessels (fig. 20, LB; fig. 48, LV), about 11 μ in diameter, parallel with and slightly ventral to the intestine. They lie adjacent and ventral to the nerve cords (figs. 14, 17, 18, and 19, LV). In the esophageal region the two vessels begin to converge and soon pass through the brain ring, one on either side of the proboscis. Immediately dorsal to the posterior end of the rhynchodaeum the two vessels are united in a cephalic commissure (fig. 20, AB). At the posterior end of the body the vessels are likewise joined by an anal commissure (fig. 15, BC) ventral to the intestine. In one adult worm the anal commissure was 125 μ anterior to the hind end of the body, in a position anterior to the anal commissure of the lateral nerves. There is no trace of a dorsal vessel.

The walls of the blood vessels consist of a very thin endothelium placed upon an extremely delicate basal membrane, external to which there is a thin layer of circular muscle fibers. In living worms the vessels are capable of contractions independent of the movements of the body wall muscles. As a result of these the walls of the blood vessels are thrown into numerous bulges and bulbous projections. These can be seen well in both living and sectioned material. The bulbs contract strongly and rapidly, beginning usually at the anal commissure and progressing some distance anteriorly. Any given section of the lateral vessels, however, may initiate short waves of contraction of its own accord. An optical section of a lateral vessel shows structure which apparently comprises transverse partitions, dividing the vessel into chambers. However, by focusing above and below the plane, it can be shown that these are not septa but only the infolded edges of the vessel wall. The cavity of the vessels is thus continuous. Occasionally minute granules are seen floating about in the fluid which fills the vessels. No blood cells could be identified, using the technique available.

The simple type of circulatory system found in *C. c. imminuta* and in other members of the genus Carcinonemertes, lacking the dorsal vessel, a condition found in only one other hoplonemertean, *Balaenanemertes chuni* Bürger (1909, p. 211), forms a striking contrast with the greatly ramified blood vessels found in the commensal nemertean *Malacobdella grossa* (Müller), a description of which may be found in the work of Riepen (1933).

Excretory System.—The excretory system in *C. c. imminuta,* and indeed in the entire genus, if it exists as a morphological unit, is unknown. The writer was unable to discover any trace of an excretory apparatus, either in the live worms or in sections. The absence of an excretory system is not confined to this genus. The pelagic Polystilifera (Pelagonemertes, Nectonemertes, etc.) lack this apparatus, and probably also

does the monostiliferan, littoral genus Prosodenoporus. However, future cytological investigations may demonstrate the existence of such a system. This was the case in Cephalothrix, which was believed to lack nephridia, until Coe (1930) demonstrated the presence of metanephridia probably homologous to those of the annelids.

Nervous System.—The nervous system consists of a four-lobed brain (fig. 20, B), embedded in the parenchyma near the anterior end of the body. From this arise two lateral nerve cords (fig. 20, LN). These extend posteriorly along the sides of the body in the parenchyma between the intestine and the submuscular glands (figs. 14, 17, 18, and 19, LN), and finally unite in an anal commissure (fig. 15, NC) ventrally to the terminal part of the intestine. The brain is composed of four ganglia, a dorsal and a ventral ganglion on each side, united dorsally and ventrally by commissures (fig. 16, VC and DC). Thus there is formed the brain ring, about 20 μ in diameter, through which the proboscis and blood vessels pass. The esophagus lies directly below the ventral commissure.

In the living worms the brain lobes, situated a short distance posteriorly to the ocelli, are transparent to whitish, occasionally light flesh colored, with fine longitudinal striae. In eight worms the lobes varied from 65 to 106 μ in diameter, averaging 83 μ. The dorsal and ventral commissures are approximately 38 μ in width, measured in an anterior-posterior direction. From the anterior faces of the dorsal ganglia there arises on each side a nerve (fig. 20, ON) about 9 μ in diameter, which passes anteriorly to supply the head region and ocelli, which are embedded in the tissue of the head. These ocellar nerves, situated about 60 μ apart, can be followed for only a short distance, usually about 20 μ, when their branches become lost to view in the opaque parenchyma and gland cells. The ventral lobes of the brain taper rather sharply posteriorly to form the lateral nerve cords (fig. 48, LN). These, measuring 13 μ in diameter, can be followed several hundred microns posteriorly, but become increasingly difficult to distinguish because of the obscuring submuscular glands, gonads, and intestinal pouches. There is no dorsal nerve, and the writer was unable to identify morphological units of any other sensory structures.

Female Reproductive System.—In the female the reproductive system is very simple, consisting merely of a series of sacs alternating with the intestinal lobes (fig. 34) and reaching from a short distance behind the anterior end of the intestine to the posterior end of the body. Each sac is bounded anteriorly and posteriorly by the intestinal pouches, while ventrally, dorsally, and laterally it is contiguous with the submuscular glands. When the ovaries are ripe and distended with developing eggs, the submuscular glands may be pushed aside and the walls of the ovaries brought into contact with the longitudinal muscle layer. The ovaries

at the extreme ends of the series are smaller and not as productive as the others. As may be seen in Table 4, the number of ovaries varies directly with the length of the worm. An adult worm 0.420 by 0.098 mm had 8 ovaries on the left side and 7 on the right, while a large mature worm 35.0 by 0.3 mm had 185 pairs of ovaries. The stage of development reached by the eggs of each ovary is nearly uniform throughout the body of any one individual, although there is some variation in this respect.

Some ovaries were seen which were nothing but large, thin-walled sacs, the lumen of which was empty of all solid materials (fig. 49). Evidently the eggs had just been shed from these ovaries, although no trace of ruptures or ducts to the exterior of the worm could be seen.

As already mentioned, worms taken from the gills of the crabs often show rudimentary gonads, in which little differentiation of the ovaries has occurred. In sectioned material they are seen to be solid clusters of cells. Sexually ripe worms, however, have sac-like ovaries, in whose walls the oogonia are situated. In the lumen of the sac can be seen eggs in the 1, 2, 4, 8, and sometimes 16 celled stage. McIntosh (1873-1874, p. 93) stated that in *C. c. carcinophila* he found ciliated embryos within the body of the parent worm, but this condition was not seen by the writer in *C. c. imminuta*. The number of eggs in any one ovary ranged from 1 to 7, with many younger eggs still in the walls of the ovary.

Male Reproductive System —Since a detailed description of the male reproductive system in the genus Carcinonemertes was published (1941b) by the writer in the Journal of Morphology, only a brief account of the male system in *C. c. imminuta* will be given here. From each of the numerous oval testes which lie in the space between the intestinal wall and the submuscular glands there arises a delicate duct, the vas efferens. The many vasa efferentia are directed toward the mid-line of the body just dorsal to the intestine, where they empty into a long median duct, the vas deferens. Near the posterior end of the body the narrow vas deferens enlarges to form a seminal vesicle, filled with spermatozoa. At the posterior end of the seminal vesicle the vas deferens resumes its former narrow diameter, makes a loose single loop, and passes to the dorsal side of the posterior end of the intestine. There the vas deferens empties into the lumen of the intestine, forming in reality a cloaca. Spermatozoa are present throughout the male system. There is a thick ridge of cells projecting centrally from the mid-dorsal part of the body wall which accompanies the vas deferens from its anterior origin to the beginning of the seminal vesicle. It is present only in male worms and its function is not certainly known. Since Takakura (1910) was the first to recognize the existence of this unique male reproductive system, the writer proposes to refer to the vas deferens with its efferent ducts

as Takakura's duct. This type of male reproductive system is present only in the genus Carcinonemertes among the Nemertea. The writer has found no evidence for the support of Takakura's hypothesis that the vas deferens is a part of the proboscis which has become pinched off from the small anterior part and has come to serve another function. Takakura's duct is evidently in no way homologous with the posterior part of the proboscis, but is a structure of separate origin.

Distinctive Characters of C. c. imminuta.—*Carcinonemertes carcinophila imminuta* differs from *C. c. carcinophila* (Kölliker) in its smaller size, shorter and more slender basis, and shorter stylet. A tabular comparison of the two closely related varieties is given in Table 7. Although the differences appear at first glance to be minute, they have been studied in great detail and have been found to be constant. It should be noted that there is no significant difference in the ratio of stylet to basis.

DEVELOPMENT AND BIONOMICS

In discussing this topic references will be freely made for the sake of completeness to work published on other members of the genus, especially *C. c. carcinophila*. The latter is so closely related to the variety under immediate consideration that any data regarding it should be taken into account.

Copulation and Insemination.—The process of copulation, leading to the fertilization of the eggs, has been described in this genus by Coe (1904a, p. 552) as follows: "In Carcinonemertes a number of writers have observed the male and female worms to place their bodies side by side, either in an outstretched condition or somewhat folded, and then to secrete a large amount of mucus which encloses the bodies of both worms in a common mass of secretion. The eggs are then deposited from both sides of the body of the female and are fertilized by the sperm discharged simultaneously by the male. Sometimes several of each sex,

TABLE 7.—COMPARISON OF *C. c. imminuta* WITH *C. c. carcinophila*

	C. c. imminuta		C. c. carcinophila	
	Extremes	Average	Extremes	Average
Length of basis.....	19–23 μ	21.0 μ	19–30 μ	25+ μ
Diameter of basis...	4.5–6 μ	5.3 μ	6–8 μ	7 μ
Stylet length.......	6–9.5 μ	7.3 μ	6–12 μ	9 μ
S:B ratio..........	0.272–0.461	0.347	0.316–0.400	0.358
Body length........	0.42–35.0 mm	about 15 mm	20–70 mm	about 30 mm?

sometimes a single male and a single female participate in this act. If it happen that a portion of the eggs in any of the ovaries are retained within the body of the female, such eggs are fertilized by spermatozoa which enter the openings into the ovaries." The process of copulation and ensuing insemination was not observed by the writer in live worms. In fact, during the course of the numerous observations, a male and a female were never seen together in the same mucous sheath. It seems probable that this does occur, however, since otherwise sufficient numbers of spermatozoa would be unlikely to locate the female on account of the dilution of the spermatozoa in the sea water. That males and females in this genus do at times occur together in the same sheath is beyond doubt, for in sections of the new species to be described below there is one which shows both sexes in the same sheath.

The great numbers of spermatozoa present in the seminal vesicle of the male are probably forced out through the anus by the contractions of the body wall, the vesicle itself undergoing no contractions. The mucous sheath surrounding the two animals retains the spermatozoa in close proximity to the female, whose ovaries they then enter.

Early Cleavage Stages.—The eggs are formed in the walls of the ovary and later come to lie free in the lumen of the ovarian sac (fig. 17, O). The walls of the latter contain both oogonia in various stages of development and yolk granules (fig. 17, W). Unfertilized eggs are infrequently seen. One such egg measured 58 μ in length and somewhat less in width (fig. 37). Its cytoplasm was very finely granular. Its clear transparent nucleus, measuring 17 μ in diameter, contained a grayish body (nucleolus) 8 μ in diameter. The cell membrane was the only external covering. Fertilized eggs (fig. 38), possessing a thin hyaline fertilization membrane, measured 55 μ in diameter with grayish nuclei (fusion nuclei) 16 μ in diameter. The cytoplasm was more coarsely granular than previously with numerous small vacuoles. Van Beneden (1861, Pl. III, figs. 14 to 16) and McIntosh (1873-1874, Pl. 17, fig. 19) have both given drawings of the eggs of *C. carcinophila.*

The two-celled stage (fig. 45), measuring 63 by 43 μ, with nuclei 12 μ in diameter, has cytoplasm and nuclei similar in texture to the one-celled stage. The second cleavage plane, at right angles to the first, divides the egg into four equal blastomeres (fig. 39), each about 33 μ in diameter, with nuclei 5 μ in diameter. The egg, measuring approximately 71 by 50 μ, is now flattened in a polar direction (fig. 10).

The third cleavage plane is equatorial (fig. 8) and divides the egg into eight blastomeres, each 26 to 27 μ in diameter, with minute nuclei which cannot be definitely made out in the living state. The upper four blastomeres lie in the grooves between the four lower ones, indicating

that the cleavage is probably of the spiral type. The egg has now regained its original spherical shape. The blastula (fig. 46), containing numerous small blastomeres 12 to 13 μ in diameter, measures 78 μ in total diameter. No embryos beyond the blastula stage were seen in the body of the parent worm. Succeeding stages were all outside the body. According to McIntosh (1873-1874, pp. 93-94) the embryos of *C. carcinophila* are sometimes retained in the body of the female. He wrote, "Many of the parents with developing young in their interior are feeble, and almost in a decaying condition inside the sheaths, so that the inert bodies seem but the nidi for the growth of their progeny . . . . "

Late Embryos and Egg Cords.—The embryos, still inside the egg membranes, are shed by the mother worm and are cemented to the inner surface of the walls of the mucous sheath by mucus, which hardens in the water to hold the eggs firmly in place. The worm then retreats from that area of the sheath, and the latter collapses to form a solid cord of eggs (fig. 21), each egg containing a developing embryo. All the embryos present in one egg cord are in nearly identical developmental stages, indicating that they were all extruded from the same female worm at about the same time. Both Van Beneden (1861, Pl. III, figs. 17 and 18) and McIntosh (1873-1874, Pl. 16, fig. 18) showed embryos in the egg cords of *C. carcinophila.*

The embryos soon develop cilia and ocelli, and begin to rotate inside their egg membranes (fig. 44). However, the embryos in some eggs may not show ocelli until they reach the free-swimming stage. The diameters of 20 eggs gave an average diameter of 75 μ, with extremes of 67 μ and 84 μ. These embryos possessed two irregularly shaped ocelli, 3.6 by 5.4 μ. They rotated for 60 hours in a finger bowl of sea water at a temperature of about 80 degrees Fahrenheit, after removal from the egg mass of the crab. The addition of clean water caused the embryos to speed up their rotations. Normally in clean sea water they rotated once every two seconds. No internal differentiation of structure other than the ocelli could be seen in the living specimens. The body is grayish and filled with numerous globules and granules of various kinds. McIntosh (1873-1874, p. 93) stated that in *C. carcinophila* "the embryo in each is sometimes ciliated on the tenth day (Pl. 16, fig. 20), although entire dependence cannot be placed on this date, since development occurs within as well as without the body of the parent." The embryos lie uncoiled in the egg membranes. Bulging movements at each end of the embryo rupture the delicate surrounding membranes and the embryo, now a free-swimming larva, swims forth with its cilia beating rapidly.

Free-swimming Larva.—Immediately after hatching, the body is spherical and of the same size as it was while in the egg. The cilia beat

rapidly and the anterior cirrus, located terminally, whips around actively. Soon, however, the larva elongates (fig. 25), and the posterior cirrus can be plainly seen on the terminal part of the body. The anterior and posterior cirri are evidently formed while the embryo is still in the egg membranes, but they are not evident until after hatching. The larvae spiral in their course, all the while being propelled ahead in a zigzag line. The two cirri wave back and forth during swimming, and the cilia beat continuously. Swimming is accomplished by means of both cilia and cirri. The movement of the cilia accounts for the rotating motion, like that of a ciliate protozoan, while the whipping back and forth of the cirri accounts for the zigzag movement, resembling that of a flagellate protozoan. The anterior cirrus is about twice as long as and more active than the posterior one. The measurements of five free-swimming larvae are shown in Table 8. Most of the larvae are slightly flattened dorso-ventrally. One larva, 134 by 64 μ, contracted under pressure to a spherical shape with a diameter of 84 μ, possibly indicating that muscle fibers are already differentiated at this early stage. The cilia covering the body measure 6 μ in length, or about the same length as in adult worms. Each cirrus is made up of at least three long thread-like elements which normally work in unison as one cirrus (fig. 5). Under pressure the elements sometimes become separated. The cirri were first mentioned by Van Beneden (1861, p. 22), but nothing was known of their multipartite nature.

In living larvae very little structural differentiation can be seen. The two brownish yellow ocelli, which may be very minute (only 1 or 2 μ in diameter) or altogether absent, are made up of clusters of small granules. In a larva 130 by 70 μ, the ocelli were located 18 μ apart at a level 22 μ from the anterior end of the body. The larva is covered with a ciliated integumental epithelium about 7 μ in thickness.

Many writers have gone on the assumption first made by Van Beneden (1861, pp. 22-23) that in C. carcinophila the outer ciliated coat is

TABLE 8.—MEASUREMENTS (IN MICRONS) OF FREE-SWIMMING LARVAE OF C. c. imminuta

Length	Width	Anterior Cirrus	Posterior Cirrus
126	97	50	25
138	100	60	34
105	46	28	13
134	64	46	24
130	70	41	20
126.6	75.4	45	23.3

shed before the definitive worm appears. Van Beneden's account of this was as follows:

Les cils vibratiles sont devenus maintenant si nombreux, qu'ils forment une toison autour du jeune ver, toison qui tombe aussitôt après et emporte le filament qui semble lui avoir servi de sentinelle au début de la vie. Le jeune ver, après cette mue, n'a pas changé de forme, conserve les deux points oculaires et n'a subi d'autre changement que celui de la perte de l'organe exploratif dont nous nenons de parler. C'est le moment de nous demander: est-ce une mue que le ver subit ou bien est-ce un scolex qui a engendré un proglottis? Nous penchons fortement en faveur de cette dernière interprétation, d'autant plus que l'analogie des vers distomes, aussi bien que des cestoïdes, lui est favorable. La première forme, avec ses deux filaments à un ou deux pôles, représente l'enveloppe ciliée des jeunes distomes à leur éclosion, et la vésicule hexacanthe du premier âge des Cestoïdes, ou enfin les Pilidium, étudiés avec tant de soin l'année dernière par MM. Leuckart et Pagenstecher.

The same author showed a figure (Pl. III, fig. 28) of a three-day old larva ("embryon, âgés de trois jours") which has lost the outer coat of cilia supposedly and the cirri.

Concerning the shedding of the ciliated epithelium, McIntosh (1873-1874, pp. 93-94) wrote:

[Van Beneden] fell into the error of supposing that a form having a smooth outline was developed within its progenitor with the long ciliary tuft, the former representing the *scolex,* and the latter the *proglottis;* in short, as he says, a case of digenesis, and not a metamorphosis. But his drawing represents the so-called *proglottis* furnished with two eyes exactly in the same manner as the *scolex,* yet he neither mentions having seen the one form inside the other nor figures this interesting condition. No such mode of development has ever been seen by me, either in the case of those ova deposited in the unimpregnated condition or in those developed within the body of the parent; but the same gradual changes ensue in the young of this animal as in Tetrastemma, and, as will afterwards be seen, also in Cephalothrix.

Dieck (1874) claimed that in *Cephalothrix galatheae* Dieck (? — *C. carcinophila*) the larval integument with its cilia and cirri is shed.

Since the writer was unable to keep the free-swimming larvae alive in the laboratory until they settled down to a crawling existence, no observations on the morphological changes could be made. One thing is certain, however, that the anterior and posterior cirri are lost during the metamorphosis. The smallest crawling worms seen showed no traces of them. The whole subject of metamorphosis in this species is one which urgently requires investigation. At present McIntosh's interpretation, based as it is upon actual observations, seems to the writer to be more reliable than any other.

The granular interior of the larva contains in the posterior region numerous clear globules measuring 4 μ in diameter. Smaller globules of various sizes are scattered through the body. A clear bilateral area posterior to the ocelli probably represents the brain rudiments, while an indefinitely defined central area indicates the position of the esophagus and proboscis. Van Beneden (1861, Pl. III, fig. 28) mistook the esophageal region in the European *C. carcinophila* for the mouth.

When a heavily infested egg mass of a crab is placed in a finger bowl of sea water, thousands of free-swimming larvae emerge within an hour or two from among the crab eggs and swim to the side of the dish nearest the source of light. They are, then, positively phototactic, in contrast to the negative phototaxis of the adult worms. The larvae did not survive more than a day or two, even with many changes of water. The unavoidably high temperatures in the laboratory in which they were kept, ranging from 70 to 95 degrees Fahrenheit, probably were a factor contributing to their mortality.

Immature Worms.—Very minute worms, negatively phototactic like the adults, were found crawling about on the egg masses of the crab. These were more numerous on the older, dark brown or black egg masses than on the younger, light yellow or orange eggs. The smallest, taken from an orange egg mass, measured 300 by 88 μ. The intestine, filled with a brownish, granular material, was a simple sac with no lateral pouches. The ocelli were very irregular in shape, and not distinctly separated. The basis measured 20 by 5 μ and the stylet 5 μ in length. Unfortunately this specimen was crushed before a camera lucida drawing could be made.

Another worm (fig. 20), measuring 0.378 by 0.126 mm under pressure of a cover glass and 0.273 by 0.084 mm without pressure, had a basis 21 by 5.5 μ and a stylet 6 μ long. The body was highly contractile. There were two ocelli 13 and 19 μ in diameter respectively. Brain, lateral nerve cords, blood vessels, intestine, and esophagus were all completely formed though not of mature size. No traces of gonads could be seen. The middle proboscis chamber was 15 μ in diameter and the posterior chamber 38 by 19 μ.

A third immature worm, 336 by 155 μ, had four irregular ocelli, each 8 to 9 μ in diameter. The basis and stylet were not well formed. The proboscis chambers were distinct, however. The intestine was a brownish, central mass, and the brain lobes were conspicuous.

Between the sizes of the largest free-swimming larva (138 by 100 μ) and the smallest immature worm observed (278 by 84 μ) there must occur a great deal of differentiation of organs in the body. The alimentary canal, proboscis, nervous, circulatory, and muscular systems are all formed almost completely during that time, although rudiments of these systems are probably present early in the free-swimming larva or even in the unhatched embryo.

The smallest sexually mature female worm observed (fig. 34) was 0.420 by 0.098 mm. Its sheath was creased longitudinally and had no raised lapilli. Several eggs were scattered along the inner wall of the sheath and many more were present in the body of the worm. The smallest adult male worm observed was 0.928 by 0.131 mm. Although the worms may mature at the small sizes just mentioned, the length of

the body continues to increase. Worms from the gill lamellae of the crab ranged from 0.777 to 33 mm. In many of them rudiments of gonads could be seen when observed in the living state. Sections of these worms showed the presence of immature gonads also.

Table 9 shows some of the growth changes which occur in the developing worms.

The ocelli increase in size. The middle proboscis chamber and the posterior proboscis chamber are noticeably smaller in the worms under 1.5 mm in length. In worms less than 1 mm the esophagus appears to be small and weak. The measurements of the basis and stylet in minute worms and large adults do not seem to differ much. In correspondence with the writer (November 8, 1940) regarding the size of the basis in nemerteans, Dr. Coe wrote: "I have found during recent years the most surprising differences in the size and proportions of stylet and basis in individuals of different ages and size in the same species. By experimental studies I find that the basis and all accessory stylets are sloughed off from time to time during growth and replaced by those of longer size as growth proceeds. There is a general correlation between size of worm and size of basis but it is not always very close." Whether such is the case in *C. c. imminuta* is not known, and the observations of the writer show nothing to substantiate such a course of events. In fact, the data

TABLE 9.—MEASUREMENT OF GROWTH CHANGES IN *C. c. imminuta*

Length (mm)	Width (mm)	Basis (μ)	Stylet Length (μ)	Diameter of Ocelli (μ)	Diameter of Middle Proboscis Chamber (μ)	Posterior Proboscis Chamber (μ)	Esophagus (μ)
0.300	0.088	20 x 5.0	5.0	. .	. . .	. . . . . .	. . . .
0.378	0.126	21 x 5.5	6.0	13, 19	15	38 x 19	. . . .
(0.278 x 0.084 without pressure)							
0.573	0.180	22 x 4.5	5.5	17	. . .	. . . . . .	35 x 28
0.629	0.164	22 x 5.0	6.0	28	24	37 x 37	distinct
0.647	0.233	20.5 x 4.5	6.5	. . .	10	18 x 18	. . . .
(0.518 x 0.148 without pressure)							
0.740	0.259	22.5 x 5.5	6.0	20	17	22 x 17	. . . .
0.777	0.150	22 x 5.5	6.5	. . .	. . .	. . . . . .	. . . .
0.814	0.222	21 x 5.5	6.0	. . .	. . .	. . . . . .	. . . .
1.100	0.190	21 x 5.5	7.0	. . .	. . .	. . . . . .	weak
1.220	0.140	22 x . . .	6.0	20	38	85 x 70	147 x 120
1.387	. . . . .	20 x 4.0	7.0	13	. . .	. . . . . .	. . . .
1.424	0.095	21 x 4.5	5.0	5	. . .	84 x 67	138 x 151
10–20	0.360	21 x 5.3	7.3	20–70	35	139 x 47	178 x 97

available indicate that the basis and stylet are formed early in development and apparently at their maximum size.

Morphology and Life History of the Host, Callinectes sapidus.—A brief account of the morphology and life history of the blue crab, *Callinectes sapidus* Rathbun, is necessary here in order to bring in information relevant to the elucidation of the life history and host relationships of *C. c. imminuta*. It is upon this crab that the nemertean lives commonly at Grand Isle, Louisiana.

The branchial chambers of *Callinectes sapidus* are morphologically a part of the exterior of the body. The dorso-lateral edges of the carapace covering the thorax have been extended laterally and ventrally, meeting the bases of the walking legs so as to enclose the gills in cavities shut off from the outside world, except for inlets and outlets for water. Each gill has the shape of an elongated pyramid and consists of 200-300 separate lamellae, to which the venous blood is carried by the dorsal afferent veins. Each lamella of the eight pairs of gills is covered with a thin layer of chitin which is continued over the outside of the afferent and efferent blood vessels. The lamellae are ornamented with various projections along the outside edge (text fig. 2), which serve to keep the lamellae separated from one another. The gill chitin is continuous with the chitinous covering of the body, and as such is cast off at each ecdysis. Nemerteans encapsuled between the lamellae are cast off also. This was demonstrated by the writer by infesting young crabs with nemerteans which had been previously stained with Nile blue sulphate, after the method of Loosanoff (1937) and Vernon (1937). The stained worms were found on the gills of the exuvium.

The water enters the gill chambers, according to Truitt (1939) and the writer's observations, through slits at the bases of the chelipeds, and, after passing over the gills, is forced out of the chamber through the exhalent opening above the bases of the second maxillae. The three flabella (epipodites) of the maxillipedes assist the scaphognathite in its action of baling out water from the gill chamber.

Solid particles are often found in the gill chambers. Grains of sand, many commensal barnacles (*Octolasmis mülleri* (Coker)), bryozoans, and in one case a specimen of Nereis 3 cm in length have been found by the writer.

The gill chambers afford a splendid habitation for the animals which live there. They are protected from their enemies of the outside world, have abundant food and dissolved gases for respiration brought to them, and their waste products are carried off. The chief disadvantages are that they live only as long as the host lives and that they are thrown off the host when the crab molts.

The first two abdominal segments of the adult male bear special-
ized appendages. In the adult female there are four pairs of pleopods,
bearing long hairs. The eggs of the crab are attached only to the hairs of
the endopodites, never to those of the exopodites. The mechanism of the
attachment of the eggs in a related crab has been described by Yonge
(1938). When the crab has come into "berry," i.e., when it is ovigerous,
the abdomen is extended posteriorly, and the pleopods wave back and
forth almost constantly. The eggs when first laid are light yellow to
orange, but as the chromatophores of the crab embryos develop the
whole egg mass becomes dark brown or almost black in some cases.

The most thorough investigation of the life history of *C. sapidus* is
that of Churchill (1919), conducted at Chesapeake Bay, Maryland, which
combined data from Binford (1911) and included much new material.
The crab embryos require about fifteen days to hatch from the eggs
attached to the pleopods of the mother. The ensuing free-living zoea and
megalops stages occupy about one month. From the megalops to the
adult about fifteen moltings occur, with an average time between molts
of 15 days, ranging from 6 days for the early stages to about 25 days
for the last. The crabs become mature and mate during the second
summer, when about 12 to 14 months of age. The female does not molt
after reaching sexual maturity. The spermatozoa she received during
copulation at her last molting suffice to fertilize two or more successive
lots of eggs. The usual life span is probably about three years. During
copulation the male carries the female about and holds her for hours or
sometimes even days (Chidester, 1911).

In a statistical study of molting in *C. sapidus* in Chesapeake Bay,
Maryland, Gray and Newcombe (1939) found that, starting with the
initial size of 20 mm in width, the male crabs molted eleven times, two
more than the number for females of the same initial size. The latter
apparently do not molt after becoming sexually mature, while the males
undergo at least two additional molts.

Callinectes sapidus is found from Nova Scotia (Piers, 1933) to
Uruguay (Rathbun, 1930). It is extremely abundant in the region of
Grand Isle, Louisiana, being by far the most commonly found of the
larger invertebrates, with the exception of the oyster which is cultivated
there. It is more abundant throughout its range in estuaries, where it
sometimes invades brackish or even fresh water. Gunter (1938) found
an immature male in the Atchafalaya River at Simmesport, Louisiana,
on August 4, 1937, a locality 160 miles from the Gulf of Mexico.

The blue crab will live out of water only a short time. Pearse (1928-
1929) reported 28.5 hours as the maximum time in air and again (1936)
reported an average out of 14 crabs of 34.4 hours and a maximum of 97.3.

Churchill (1919) observed that the females migrate to water of

higher salinity when ready to lay their eggs. After the young are hatched, the females may migrate back to the fresher water. The males tend to remain in the shallow regions of rather low salinity, where they copulate with the virgin females which are constantly arriving from the regions of higher salinity. In the winter the females and probably a good many of the males also go to deeper waters (Churchill, 1919, and Cowles, 1930) where they lie dormant on the bottom. Nothing is known regarding the extent or rapidity of migration in *C. sapidus.* The tagging experiments of Meek (1913) showed that in England the common crab, a close relative of *C. sapidus,* may migrate as much as 28 miles in 36 days, a considerable speed and distance. Such migrations would bring about widespread distribution of any nemerteans which the crabs might be carrying at the time.

The area in which the specimens of *C. sapidus* were collected comprised about 400 square miles in the vicinity of Grand Isle, Louisiana. Grand Isle separates the island-dotted Barataria Bay from the Gulf of Mexico, except for the various passes, Caminada Pass, Barataria Pass, or Grand Pass as it is sometimes called, Quatre Bayou Pass, and other smaller ones. The depth of the water in Barataria Bay seldom exceeds 10 feet, although in the passes to the open Gulf it may reach 60 feet. Much of the bottom in the bay, composed of sand and silt, is devoted to oyster culture. Innumerable shallow mud flats and marshy inlets are found around the islands. Outside in the Gulf proper the bottom is predominantly sandy, with still a good proportion of mud near the shore. The turbidity is much less than in the bay region. The pH range, determined in the field colorimetrically, of samples from Barataria Bay and from offshore in the Gulf was 7.6 to 8.4. The bottom in the Gulf slopes off from Grand Isle very gradually until about three miles offshore, when the slope becomes much steeper. At three miles the depth is only about 15 to 20 feet, while at twelve miles it reaches 40 to 50 feet. The temperature of the water ranged from 25.8 to 29.8 degrees Centigrade. The salinity, determined by the silver nitrate titration method as outlined by Johnstone (1928), was progressively higher as one proceeded from the extreme northern reaches of the bay toward the Gulf. At Chene Fleurie in the extreme northern part of Barataria Bay the salt content was only 9.18 grams per liter. Southward in the bay near Manila village the salinity was 19.23, at Bayou Fifi at the eastern end of Grand Isle it was 25.30, and five miles south of Grand Isle it was 29.32 grams per liter. The specific gravity varied correspondingly with changes in the total salt content (True, 1915). The readings of both salinity and specific gravity were checked by the formulae and tables given by Knudson (1901).

Life History of C. c. imminuta.—The writer was unable to demon-

strate the life history of this nemertean in the laboratory because of
the brief time available for work at Grand Isle and because of the lack
of suitable laboratory apparatus for maintaining crabs and worms alive.
However, by fitting together statistical information on infestations in
the crabs and observations of the various immature stages of the worms
with the life history of the crab, some deductions can be made which
reveal in a general way the life history of this nemertean.

The time required after fertilization before extrusion of the develop-
ing eggs from the body of the female is unknown, but is probably only
a few days. McIntosh (1873-1874) believed that the eggs in the egg
cords of the European *C. carcinophila* require about ten days before
hatching occurs. During that time the egg cords are waved about and
kept clean of other organisms and debris by the movements of the
pleopods. The time for hatching of *C. c. imminuta* is probably shortened
in the warm Gulf waters. The free-swimming larvae hatch from the egg
by making bulging movements which rupture the egg membranes. After
a short time the larvae begin to elongate and the anterior cirrus, present
when the larva is hatched from the egg, is followed by the appearance
of a posterior cirrus. The eye spots, often present in embryos while still
in the eggs, are nearly always present in the free-swimming larvae. The
larvae swim actively about, and are capable of scattering over a consider-
able area by their own movements. A large proportion of the larvae are
probably washed away from the egg mass of the host crab by the currents
set up by the beating of the pleopods. The escape from the host egg mass
and wide distribution in the water may be aided by the positive photo-
taxis of the larvae. The ventral side of the crab abdomen among the
eggs is dark in comparison with the brighter surrounding water. Then,
too, the surface water is more brightly lighted than the water near the
bottom. The larvae therefore are doubtless stimulated to swim out from
the egg mass and toward the surface of the water. There they may come
in contact with (1) the gills of immature male crabs, (2) the gills of
mature males, (3) the gills of immature females, (4) the gills of mature
females, or (5) the egg masses of adult females. Some of the larvae may
remain on the original egg mass and develop into the crawling worms
there. Van Beneden (1861) stated that in the European *C. carcinophila*
the embryo three days old, i.e., the free-swimming larva three days old,
has then already lost its cirri and settled down to a crawling existence.

The shallow water, the relative lack of strong currents in the Bara-
taria Bay region, and the abundance of crabs (in some areas estimated
to be at least one crab in every 100 square feet of bottom) all seem to
aid the larvae in coming in contact with the bodies of crabs which are
potential hosts.

The time required from fertilization until the hatching of the free-

swimming larvae from the eggs (about 11 days) is well within the time required for the crab eggs to hatch (about 15 days). The period of about three days needed for development of the free-swimming larvae before they settle down to the definitive crawling state, added to the previous time makes a total of about 14 to 15 days from fertilization until the larvae are capable of infesting other crabs. This time, necessary for the development of the worms, is probably considerably shortened in the warm waters of the Grand Isle region.

The fate of the free-swimming larvae varies. Many of them probably never come in contact with a suitable crab host, and eventually die. Some of them, no doubt, are eaten by fish and various invertebrates. Those which do succeed in reaching a crab have only about two chances out of five of its being one on which they can become mature, i.e., an adult female either with or without an egg mass.

In order to determine the incidence of the nemerteans on *C. sapidus* and the correlation with sex, age, and molting, 819 crabs of both sexes and in various stages of maturity were examined during the months of June and July in the vicinity of Grand Isle in 1939 and 1940. The results are shown in Tables 10 and 11.

Table 10 shows that the immature male crabs were uninfested with *C. c. imminuta,* although one such crab had *Octolasmis mülleri* (only a single specimen, however, and that not mature). The adult males, i.e., those over 89 mm in width, according to the standard of Gray and New-combe (1939), showed a light infestation with the barnacles in about 18% of the total number examined. Those males from the Gulf were more frequently infested with barnacles than those from Barataria Bay. In each individual the infestation never exceeded 20 barnacles. The number was usually much less, and often those present were immature. Two mature males had a few minute nemerteans on their gills. These were all less than 1 mm in length. The smallest mature male crab infested was 10.9 mm in total spine to spine width. One of the worms recovered from its gills was 0.573 by 0.180 mm. The total percentage of males infested was only 0.97%. A single male had both barnacles and nemerteans in the gill chambers.

The immature female crabs were likewise extremely lightly infested. One such crab had a single nemertean, two others had both nemerteans and barnacles, while two more had only barnacles. The infestation by both worms and barnacles was very light. The smallest infested immature female crab was 9.1 mm in total spine to spine width. The smallest worm recovered from the gills of an immature female was 0.777 by 0.150 mm and none exceeded 1.5 mm in length.

These incidence data may be interpreted easily by recalling the known facts of the life history of *C. sapidus.* The younger the crab is, the

TABLE 10.—INCIDENCE OF *C. c. imminuta* [AN]D *O. mülleri* ON *C. sapidus* AT GRAND ISLE, LOUISIANA, AND THE CORRELAT[ION] WITH SEX, AGE, AND MOLTING

	Immature Males		Mature Males		Immature Females		Mature Females without Eggs		Mature Females with Eggs	
	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent	Number	Per cent
Crabs examined:										
In Bay	10	....	118	....	42	....	79	....	49	....
In Gulf	4	....	87	....	29	....	297	....	104	....
Total	14	....	205	....	71	....	376	....	153	....
C. c. imminuta only on gills:										
In Bay	..	....	1	0.85	1	2.38	6	7.59	3	6.12
In Gulf	..	....	1	1.15	..	....	28	9.42	10	9.62
Total	..	....	2	0.97	1	1.41	34	9.04	13	8.49
O. mülleri only on gills:										
In Bay	..	....	6	5.08	2	4.76	8	10.12	4	8.16
In Gulf	1	25.00	30	34.47	..	....	36	12.12	4	3.84
Total	1	7.14	36	17.56	2	2.82	44	11.70	8	5.23
Both *C. c. imminuta* and *O. mülleri* on gills:										
In Bay			1	0.85	2	4.76	28	35.44	2	4.07
In Gulf			..	....	..	....	78	26.26	8	7.69
Total			1	0.48	2	2.82	106	28.19	10	6.53
C. c. imminuta on eggs only:										
In Bay			..		..		..		11	22.45
In Gulf			..		..		..		4	3.84
Total			..		..		..		15	9.81
C. c. imminuta on both gills and eggs:										
In Bay			..		..		..		31	63.26
In Gulf			..		..		..		16	15.38
Total			..		..		..		47	30.71

shorter is the period between molts, and the less the opportunity for the worms and barnacles to become established on the gills, since the worms and barnacles live on the exterior of the chitinous covering of the body and are thrown off at each molt. This interpretation agrees with the fact that worms and barnacles were found only on immature crabs of large sizes, and also with the fact that the infestation by barnacles was higher in the mature males than in the immature ones. It will be remembered that Gray and Newcombe (1939) found that the male crabs continued to molt after reaching sexual maturity. The longer time between molts in the mature males allows greater opportunity for the barnacles to become attached, hence the higher number of crabs infested. The nemerteans evidently are not able to live successfully in the gill chambers of male crabs, probably because of the shorter stadia, and probably also because of the tendency of the males to stay in the shallow, fresher water, sometimes in marshy pools, thereby diminishing the chances of the free-swimming larvae of coming in contact with them. The mature females, on the other hand, tend to migrate about and live in areas where the larvae can become readily disseminated. All males and immature females, of course, have no eggs, and this fact would prevent the worms from thriving on such crabs, if it is true, as the writer has concluded, that the worms feed on the crab eggs.

The mature females, in contrast to the males and immature females, are heavily infested with both barnacles and nemerteans. Of the 376 non-ovigerous females the gills of 140, or 37%, were infested with *C. c. imminuta.* Eighty-five, or 55%, of the ovigerous females were infested either on the gills or on the egg masses or both.

The non-ovigerous females showed no significant differences in infestation in Barataria Bay and in the Gulf proper. Combining the number of such crabs with nemerteans on their gills (34) with those

TABLE 11.—SUMMARY OF DATA ON INFESTATION OF *C. sapidus* WITH *C. c. imminuta* AT GRAND ISLE, LOUISIANA

Type of Crab	Number Examined	Number with .*C.c.i.* on Gills or Eggs	Percentage of Number with *C.c.i.*
Immature males	14	...	....
Mature males	205	3	1.46
Immature females	71	3	4.23
Non-ovigerous mature females	376	140	37.18
Ovigerous mature females	153	85	55.55
Totals	819	231	28.20

which had both nemerteans and barnacles (106) it is found that of the total number of non-ovigerous females, 140, or 37%, were infested with nemerteans. The number of nemerteans on any one crab was almost always large. No attempt was made to count the worms. One crab was estimated to have at least 1,000 worms of various sizes between the lamellae in the two gill chambers. Another had 640 barnacles by actual count in the gill chamber of one side. In a previous article (1941a) the writer has shown that at Grand Isle, Louisiana, the nemerteans and barnacles associate with *C. sapidus* at random and that there is evidently no relationship between nemerteans and barnacles that would favor their occurrence together on the crabs or inhibit the occurrence of one after the other has become established. The data on *Octolasmis mülleri* has been included in this discussion because it tends to corroborate the findings regarding the nemerteans.

The ovigerous females showed a light infestation in the gill chambers (23 out of 153 crabs, or 15%) and a heavy infestation of the egg masses (62 out of 153, or 40%). This indicates that the worms may leave the gills when the crab comes into berry and attach themselves in sheaths on the endopodite hairs among the eggs, where their gonads rapidly mature, the eggs are fertilized, and embryonic development takes place. The data also show that the worms probably return to the gills when the eggs of the crab are all hatched, since 37% of the non-ovigerous females had gills infested with nemerteans, but only 15% of the ovigerous crabs were so infested.

The writer found no worms living on the abdominal endopodite hairs of crabs which were not carrying eggs, although Van Beneden (1861) stated that in his study of the European *C. carcinophila* he found one nemertean 3-4 cm in length living on the endopodite hairs of a crab without eggs.

The higher infestation on the egg masses of crabs from Barataria Bay (42 out of 153, or 27%) as compared with that in the Gulf (20 out of 153, or 13%) is probably brought about by the more favorable conditions (shallow water, lack of strong currents, abundance of crabs, etc.) for the contact of the free-swimming larvae with new hosts.

In order to become sexually mature the free-swimming larvae must reach either non-ovigerous or ovigerous adult female crabs. After the larva loses its anterior and posterior cirri, it crawls but never swims. When the egg mass of the new host is hatched, the young worms migrate into the gill chambers where they encapsulate between the gill lamellae (text figs. 1 and 2). Probably none of the recently transformed young worms reach maturity on the first egg mass with which they make contact, but remain on the gills until the next batch of eggs is laid by the

crab, when they migrate out to form their sheaths attached among the crab eggs to the abdominal pleopod hairs. Churchill (1919) has shown that in *C. sapidus* there may be at least two successive batches of eggs, one in the second summer of life and another in the following summer. After the last molt occurs, at which time the female crab becomes sexually mature, all the worms which settle upon the gill lamellae remain on the body of the crab, probably for the duration of the life of the crab, which is about three years, according to Churchill (1919). The number of worms is probably increased each time that the crab berries by the settling of some of the young worms upon their mother's host. From this reasoning one would expect to find the older female crabs, which have already had one batch of eggs, more heavily infested than females which never yet have been in berry. The writer is unable to substantiate this because it is impossible to tell whether a crab has already been ovigerous and infested. There is no correlation between the size of the adult female crab and infestation with nemerteans.

Churchill (1919) stated that in Chesapeake Bay "if mating occurs quite early in the season, the eggs are laid within about two months. In the great majority of cases, however, mating occurs in July or August and the eggs are not laid until the following spring or summer." In Louisiana, however, where the water is warmer, the development of the eggs after copulation is probably hastened. At any rate there is a period of nearly two months between the last molt and the first laying of the eggs, during which many nemerteans can become settled on the gills. Perhaps a good many of the uninfested, or very slightly infested, ovigerous females are those in which the first batches of eggs, laid in the same season in which copulation occurred, are being carried, and the more heavily infested ones are those which are carrying first batches of eggs which were laid the season following that in which copulation occurred or which are carrying second or third batches of eggs. Evidence for this is suggested by the observation that egg masses which are infested by large, mature worms are generally infested by a great many such worms.

Growth of the worms probably occurs while they are on the gills, because otherwise it would appear to be impossible to account for the large sizes attained. Even if the migration to the egg masses took place twice during the life of the worm, that would allow only about thirty days for the growth of the worm from less than 1 mm to over 30 mm in length, an event which seems physiologically improbable.

The worms on the gill lamellae secrete a mucous substance by which the two lamellae are cemented together around the worm (text figs. 1 and 2). The wall of the capsule thus formed is very fragile, and when the

TABLE 12.—RECORDS OF *C. sapidus* COLLECTED DURING THE WINTER MONTHS AT GRAND ISLE, LOUISIANA, SHOWING INFESTATION WITH *C. c. imminuta*

Date	Sex of Crab	Age	Egg Mass	Barnacles	Nemer-teans
Nov. 4, 1939.............	female	adult	absent	+	−
	female	adult	absent	−	−
	female	adult	absent	+	−
	female	adult	absent	−	−
	male	adult	......	+	−
	male	adult	......	−	−
Jan. 7, 1940.............	female	adult	absent	+	−
	female	adult	absent	+	−
	male	adult	......	+	−
	male	adult	......	+	−
Apr. 7, 1940.............	female	adult	absent	−	−
	female	adult	absent	−	−
	female	adult	absent	−	−
	female	adult	present	−	+ mature
	female	adult	present	−	+ mature
Oct. 19, 1940.............	female	adult	absent	−	−
	female	adult	absent	+	+
	female	adult	absent	−	−
	female	adult	absent	+	−
	female	adult	absent	+	+
	female	adult	absent	+	+
	female	adult	absent	−	−
	female	adult	absent	+	+
	female	adult	absent	+	+
	female	young	......	−	−
Jan. 26, 1941.............	female	adult	absent	−	−
	female	young	......	−	−
	female	young	......	−	−
	female	young	......	−	−
	female	young	......	−	−
	male	adult	......	−	−
	male	adult	......	−	−
	male	adult	......	+	−
	male	adult	......	+	−
	male	adult	......	+	−
	male	adult	......	+	−
	male	adult	......	+	−
	male	adult	......	+	−

gill is removed from the crab and placed in a finger bowl of sea water the worms begin to move about. In a few minutes they rupture the walls of the capsule and crawl out over the surface of the gills.

Sexually mature worms were found abundantly throughout the last part of May, all of June and July, and the first part of August of the years 1938, 1939, and 1940. A few records of crabs collected in Barataria Bay during the winter months are shown in Table 12.

Although these data are scanty, they do show that the crabs in the Barataria Bay region are in berry nearly as late as the first of November and as early as the last part of March. (The brown eggs on the two females collected on April 7, 1940, must have been laid at least a week earlier.) Nemerteans were collected as early as April 7 and as late as October 19. Although there were no nemerteans on the crabs collected between these two dates, from November through March, it is probable that if larger numbers of adult females had been available for examination worms would have been discovered on the gills. Only seven adult females were examined during that period.

To summarize the preceding discussion, the principal events in the life history of *C. c. imminuta* during the course of one year at Grand Isle are as follows: During the months of December, January, and February, when the host is not in berry, sexually immature worms remain on the gills of the adult female crab. Growth probably takes place during this period. Toward the end of March or early April, when the first batches of crab eggs are laid, the worms migrate from the gills to the egg masses, there becoming sexually mature. A few days after fertilization, the developing eggs are extruded from the body of the female worm, and hatching of the free-swimming larvae is completed within 11 days after fertilization. After the crab eggs hatch, the adult worms may return to the gills of the crabs. The free-swimming larvae have the following possibilities: (1) they may remain on the egg mass and develop into crawling worms there within a few days, migrating to the gills when the crab eggs hatch; (2) they may never come in contact with a host crab and as a result die; (3) they may be eaten by plankton feeders; (4) they may reach the gills of a male crab, develop only a short time, and then be cast off and die; (5) they may reach the gills of an immature female and soon be cast off with the exuvium; (6) they may reach the gills of an adult non-ovigerous female and remain there over winter until the crab becomes ovigerous the following spring, when the worms would migrate to the egg mass, become sexually mature, etc.; (7) they may reach the egg mass of a female, migrate to the gills when the crab eggs hatch, and remain there until another batch of crab eggs is laid.

TABLE 13.—DECAPOD CRUSTACEANS EXAMINED FOR *C. c. imminuta* AT GRAND ISLE, LA.
(The letter "o" indicates the presence of orange egg masses, the letter "b" brown egg masses.)

Name of Crab	Number and Sex	*C. c. imminuta*
Natantia		
Caridea		
Crangonidae		
Crangon heterochaelis (Say)........	1 female	None
Reptantia		
Paguridea		
Paguridae		
Clibanarius vittatus (Bosc)..........	10 females	None
Brachyura		
Oxystomata		
Calappidae		
Calappa flammea (Herbst)........	1 female	None
Hepatus epheliticus (Linnaeus)....	2 females	None
	1 female	1 on gill (0.74 by 0.26 mm)
Leucosiidae		
Persephona punctata aquilonaris Rathbun..................	1 female (b)	3 adults on eggs (1.11 by 0.20 mm 1.66 by 0.20 mm 1.48 by 0.18 mm)
	1 male	None
Brachygnatha		
Portunidae		
Ovalipes ocellatus guadulpensis (Saussure).................	1 female	None
	2 males	None
Portunus sayi (Gibbes)...........	9 females	None
	1 female	1 minute worm (lost)
	6 females (o)	None
	3 females (b)	None
Callinectes ornatus Ordway.......	1 female	None
	1 female	5 small worms on gills
	1 female (b)	1 worm on egg mass (1 mm in length)
	25 males	None
Arenaeus cribrarius (Lamarck)....	3 females	None
	1 female	1 worm on egg mass (1.2 by 0.2 mm)
	3 males	None

TABLE 13.—Concluded

Name of Crab	Number and Sex	C. c. imminuta
Brachygnatha (concluded)		
Xanthidae		
Panopeus herbstii H. Milne-Edw...	4 females	None
	1 female (b)	3 worms, about 1.5 mm in length, and 2 empty sheaths, all on eggs
	3 males	None
Eurypanopeus depressus (Smith)...	1 female (b)	None
Eurytium limosum (Say).........	2 males	None
Menippe mercenaria (Say)........	1 female	None
	1 female (soft)	None
	4 females (o)	None
	1 female (b)	Several small worms and egg cords on egg mass
	1 female (b)	1 small worm on eggs
	1 male (soft)	None
	3 males	None
Grapsidae		
Sesarma cinerea (Bosc)..........	2 females (b)	None
Sesarma reticulatum (Say).......	2 females	None
	1 male	None
Ocypodidae		
Ocypode albicans Bosc...........	1 female	None
	2 females (b)	None
Uca minax (Le Conte)..........	2 females (b)	None
Inachidae		
Libinia dubia Milne-Edw........	1 male	None

GEOGRAPHICAL DISTRIBUTION AND HOSTS

During June and July, 1940, 108 decapod crustaceans other than *Callinectes sapidus*, almost all Brachyura, were examined for *Carcinonemertes*. These represented 18 species, and were collected within a radius of 15 miles of Grand Isle. The crustaceans examined and infestations recorded are shown in Table 13.

Seven species of Brachyura, in addition to *Callinectes sapidus* Rathbun, were found, as indicated in Table 13, infested with *Carcinonemertes carcinophila imminuta*. These are *Hepatus epheliticus* (Linnaeus), *Persephona punctata aquilonaris* Rathbun, *Portunus sayi* (Gibbes), *Calli-*

TABLE 14.—DISTRIBUTION RECORDS OF *C. c. imminuta*, BASED ON MUSEUM MATERIAL

Name of Host	Locality and Date	Length (mm)	Diameter (mm)	Basis (μ)	Stylet (μ)	S:B Ratio
Portunus spinicarpus (Stimpson), USNM 76946, 76909, 76939....	10 miles south of the Tortugas, Fla.	4.0 3.5	0.23 0.21	23.0 x 6.0 22.0 x 6.0	8.0 ...	0.347 .....
Callinectes bocourti Milne-Edwards, USNM 59281..........	Fox Bay, Colon, Panama	1.3	0.35	21.0 x 5.5	...	.....
Callinectes bocourti Milne-Edwards, USNM 24456..........	Catano, San Juan Harbor, Puerto Rico	only a fragment of a sheath				
Callinectes marginatus Milne-Edwards, MCZ 8864, USNM 7648 .	St. Thomas, West Indies, 1871 and 1884	3.5	0.28	21.0 x 5.5	...	.....
Callinectes danae Smith, MCZ 5145	Rio de Janeiro, Brazil, 1865	... ... 6.0 12.0 3.0	0.14 0.15 0.15 0.26 0.21 0.15	21.7 x 6.0 19.5 x 6.0 21.0 x 6.0 20.0 x 6.0 21.0 x 5.5 18.0 x 5.5	7.0 8.5	0.323 0.436 ....
Cronius ruber (Lamarck), USNM 59292..........	Porto Bello, Panama, Atlantic side, 1912	2.0	0.16	20.0 x 5.5	7.0	0.350

nectes ornatus Ordway, *Arenaeus cribrarius* (Lamarck), *Panopeus herbstii* Milne-Edwards, and *Menippe mercenaria* (Say). The genera Portunus, Callinectes, and Arenaeus belong to the family Portunidae, Hepatus to the Calappidae, Persephona to the Leucosiidae, and Panopeus and Menippe to the Xanthidae.

The worms on all these hosts were extremely few in number and small in size, when compared with those found on *C. sapidus,* although all were identical specifically. Therefore the writer has come to the conclusion that *C. sapidus* is the normal host for *C. c. imminuta,* at least in the Grand Isle area, and that the seven other hosts are more or less accidentally infested. It will be pointed out later that the members of the genus Carcinonemertes are generally restricted in choice of hosts to members of the Portunidae.

At Grand Isle, the infestation of the non-portunid genera, Hepatus, Persephona, Panopeus, and Menippe, was probably brought about by the extremely favorable environment for the dispersal and transfer of the free-swimming larvae. *Callinectes sapidus* is abundant and highly infested with nemerteans. These other crabs come in close contact with *C. sapidus,* allowing the infestation to be carried over. The shallow water, lack of strong currents, great abundance of crabs, and the close association of the various species of crabs all contribute to the spreading of the infestation to species other than *C. sapidus.* The data suggest that there is no host specificity. The worms will evidently thrive on almost any of the littoral aquatic crabs, if given a chance to become established there.

In addition to those records marked with an asterisk in Table 3, which may be referable to the variety *imminuta,* other records were obtained from crabs in the collections of the Museum of Comparative Zoology and the United States National Museum. These are shown in Table 14. Measurements of the body and the stylet apparatus are included wherever possible.

All these worms conform to the description given above of the variety *imminuta.* The worms from *Callinectes danae,* however, appear to be slightly larger and to possess a larger posterior proboscis chamber. In the last three of these worms listed above the posterior proboscis chamber measured 183 by 56, 140 by 77, and 160 by 50 μ respectively, being about three times the size of the same structure in fixed and sectioned specimens of *C. c. imminuta* from Grand Isle. These very slight differences may have been caused by variations in method of killing and fixing. The worms from *C. danae* were all taken from one crab, but the method of killing is unknown. A study of live worms from Rio de Janeiro will be necessary before such variations as now seem to exist can be shown to be significant.

The "worms with lateral eye spots" found by Pearse (1932) on

Bathynectes superba (Costa) at 20 miles south of Tortugas, Florida, probably were the variety *imminuta*.

C. c. imminuta has been found in the Gulf of Mexico, the West Indies, including the. Caribbean Sea, and as far south as Rio de Janeiro, Brazil.

CARCINONEMERTES EPIALTI COE

THE FIRST nemertean living on crabs reported from the Pacific Ocean was *Carcinonemertes epialti* Coe (1902a). This species was found on a kelp crab, *Pugettia producta* (Randall), formerly *Epialtus productus* Randall, collected at Monterey, California. The original description was repeated by Coe in later works (1904b, pp. 150-154; 1905a, pp. 230-233). In the latter paper he showed (Pl. 2, fig. 20) a colored figure of the worm, the first ever published. In 1905(b) and 1940 Coe again mentioned this species but gave no additional information.

The distinctive specific characteristics are as follows: Sexually mature individuals about 4-6 mm in length; proboscis very minute and short, extending scarcely more than its own diameter posteriorly to the brain; basis 27-33 μ in length and 5-8 μ in diameter, often somewhat asymmetrical; stylet 12-15 μ in length; posterior proboscis chamber bent at angle to anterior part of proboscis in ordinary states of contraction. The remaining part of Coe's original description, from which this brief list of characters has been taken almost verbatim, is occupied mainly with a discussion of generic characteristics.

The writer examined three ovigerous specimens of *Pugettia producta* in the collection of the Museum of Comparative Zoology, no. 2125 from Crescent City and no. 314 from San Francisco, California, but found no nemerteans. However, 24 specimens of *Euphylax dovii* Stimpson, a portunid crab, nos. 8766, 8765, 5464, and 8868 in the Museum of Comparative Zoology, all from Payta, Peru, yielded five specimens of *Carcinonemertes epialti* Coe. No date of collection was attached to the specimens.

The measurements of these Peruvian specimens are shown in Table 15.

In all five Peruvian specimens the posterior end of the basis is slightly larger than the anterior end (fig. 28), agreeing with the description of the basis in the Californian worms. Although the angle at which the posterior chamber of the proboscis is turned is not acute, in each worm the chamber is bent upward slightly toward the dorsal body wall. The method of fixation may have altered the relative position of the posterior chamber. The cephalic glands in the Peruvian specimens are well developed and there are distinct muscle fibers in the head region, extending in various directions around the rhynchodaeum and the anterior part of

TABLE 15.—MEASUREMENTS OF *C. epialti* TAKEN FROM *Euphylax dovii* AT PAYTA, PERU

Sex	Length (mm)	Diameter (mm)	Basis (μ)	Stylet (μ)	S:B Ratio	Middle Chamber (μ)	Posterior Chamber (μ)
Female...........	5.5	0.350	.. x 7	....	.....	42 x 34	91 x 67
Female...........	2.5	0.350	.. x 6	....	.....	30 x 23	56 x 45
Female...........	2.0	0.245	21 x 7	....	.....	25 x 19	50 x 45
Female...........	4.0	0.315	24 x 6	10.5	0.437	35 x 28	84 x 70
Immature........	1.5	0.175	25 x 7	....	.....	28 x 23	42 x 35
Averages........	3.1	0.287	23.3 x 6.6	10.5	0.437	32 x 25	65 x 52

the esophagus. Other anatomical features agree with the description of *C. epialti* given by Coe (1902a).

Although the basis in the Peruvian worms appears to be a little shorter than in the Californian specimens, such a difference probably is not significant, inasmuch as the size of this structure is known to vary somewhat individually and inasmuch as only a very few specimens were available for measurement. The ratio of stylet to basis in specimens from the two regions is nearly identical.

The mucous sheaths in which the Peruvian specimens were found resembled those of *C. c. imminuta*. The surface was covered with round or irregular lapilli, whitish in color, and of slightly different sizes (fig. 2), or with elongated, longitudinal raised areas (fig. 24). The sheaths were all a little longer than the worm in the contracted state.

CARCINONEMERTES MITSUKURII TAKAKURA

TRANSLATION OF ORIGINAL DESCRIPTION

THIS JAPANESE species has been mentioned only once in the literature, and that in the original description by Takakura (1910). Since the description was published in Japanese, it has remained inaccessible and unrecognized by students of the nemerteans, even though the paper contains the first mention of the unique male reproductive system. Therefore, the writer here presents the complete paper, with the exception of the figures, translated by Dr. Richard R. Kudo, Associate Professor of Zoology at the University of Illinois.

ON A NEW SPECIES OF PARASITIC NEMERTEAN

The so-called parasitic nemerteans are mostly either symbiotic or temporarily attached to the outside, or live inside, of other animals. There are only three truly parasitic species, in two genera. These are *Carcinonemertes carcinophila* (Kölliker)

found in the North Atlantic and Mediterranean Sea, *Carcinonemertes epialti* Coe found on the Pacific coast of North America, both on crabs, and *Cephalothrix galatheae* Dieck from Sicily on *Galathea strigosa* Linnaeus. The species under discussion was first found in Yokohama harbor in July, 1895, by Professor Mitsukuri. It belongs to the genus Carcinonemertes. At that time the harbor breakwaters were under construction and the concrete wall had cracked in places. The port authorities raised the sunken and cracked concrete blocks for examination. At that time Professor Mitsukuri collected several specimens of Lineus from the raised material, and he kindly advised me that further examination of the material might bring out valuable information concerning these worms. Therefore I went to the same locality to examine the concrete blocks brought up. In addition to Lineus, I found a very small crab that had an egg mass in which I found only two very small specimens of Carcinonemertes, a male and a female. So I waited for the opportunity to collect more material. I examined many crabs, particularly their egg masses. Finally in April, 1906, at the mouth of the Minato River, which flows into Tateyama Bay, I collected "moku gani" (small crabs, *Eriocheir japonicus* de Haan), one of which had an egg mass in which I found several dozen worms.

The body is cylindrical, filiform, with the extremities bluntly pointed and about the same in shape. There are two black eye spots located slightly back of the anterior end. The color is light brown, light yellow, or milky white. The brain in life can be seen through the tissue as a small, fleshy mass. Males and females vary in length. The extended males are only 1 cm, while extended females are three times or more as long. The maximum width for both sexes is 0.5 mm. The body secretes mucus which forms a semi-transparent tube by which the animals are attached to the bristles on the swimmerets of the host. If removed from the tube and put in sea water in a watch glass, the worm secretes mucus and attaches itself securely to the glass. Apparently this mucus is necessary to prevent the worm's being washed away by the currents.

The integument is thick, and directly below it is a thin basement membrane. There is a thin circular and a relatively thick longitudinal muscle layer, agreeing with those in other Metanemertini. Internal to the longitudinal muscles are well developed hypodermal glands, distributed over the body length, though between the longitudinal muscles and the digestive tube they become narrowed. Near the posterior end of the body these glands form a thick layer. Near the anterior end, the glands surround the rhynchodaeum and are grouped to form the cephalic glands. These open on the dorsal side of the head adjacent to the rhynchodaeum pore. The posterior part of the cephalic glands extends posteriorly to the brain. The function of these glands, both hypodermal and cephalic, probably concerns the production of mucus. In other parasitic worms similar glands produce mucus.

The digestive tract is roughly like that of other Metanemertini. The anterior end of the esophagus joins the rhynchodaeum just anteriorly to the brain. The esophagus is short and narrow, enlarged behind the brain and developing folds. Here it becomes the cardiac part of the stomach. The pyloric part follows; it has no folds. It is a narrow, elongated tube longer than the cardiac part in most species, but in this species it is very short and inconspicuous. The intestine has very wide caeca. These develop ventrally from the junction of the stomach and intestine and all around the stomach. A pair of caeca develop from the dorsal side of the stomach and reach near the brain. Along the sides of the intestine there are deep, blind sacs, which are not so deep near the posterior end.

The rhynchodaeum, i.e., from the point where the proboscis is attached to the anterior end of the head, is a narrow tube in common with the esophagus. The rhynchodaeum and proboscis are both short and extend only to the middle of the stomach. The part surrounding the rhynchodaeum is imperfect, with only thin connective tissue and without muscle layers.

The proboscis is short and thick, filling the rhynchocoel. There is no space between it and the wall. The proboscis sac is divided into three chambers. The anterior proboscis chamber has a stylet apparatus and is very short and narrow,

with no glands, although in most species of nemerteans it is long and glandular. The posterior part of this chamber, bearing the stylet, has very stout glandular walls. The stylet is small, measuring 8 μ in length. The elongated, oval basis reaches 27 μ in length. Secondary stylets and secondary stylet sacs are absent. The middle chamber has a muscular wall and large lumen. The posterior chamber is short but wide and ovoid, and glandular epithelium covers the inner surface. The anterior and posterior chambers are of different shapes, but both are short and wide. The posterior end of the hind chamber is close to the rhynchocoel wall and no muscles are attached as in other species. In *C. epialti* the posterior chamber is bent upward but in this species it is close to the ventral side.

There is a pair of lateral blood vessels, connected at the anterior and posterior ends. There is no dorsal blood vessel. The point of union at the anterior end is far posterior, as compared with ordinary species, being located immediately in front of the brain.

The excretory system as in other species of the genus is absent.

The brain is of the usual form, with right and left parts and dorsal and ventral regions. The lateral nerve cords are considerably swollen toward the posterior end of the body. The posterior commissure is on the ventral side of the posterior end of the intestine.

The reproductive organs begin behind the stomach and reach the posterior tip of the body. The testes are numerous and occur in the vicinity of the intestine. In one section there may be seen sometimes 30 testes arranged in 1 to 3 rows. Even when the reproductive elements (spermatozoa) are mature no external pores are seen. On the other hand the ovaries are arranged regularly between the caeca of the intestine on the right and left. The pores of the oviducts are located on the dorsal side of the body near the median line.

The most striking characteristic of this species is the presence of a dorsal duct running along the mid-dorsal line. It looks like a dorsal vessel but is not. The character of its wall and the relation to other organs is different.

It arises immediately behind the rhynchocoelom. Its course is similar to that of the dorsal vessel. It is a narrow tube found only in males, never in females, and reaches to the posterior end of the body. Ordinarily it is slightly larger than the lateral blood vessel, but at places it becomes very much enlarged. The posterior end obviously connects with the digestive tube immediately in front of the anal opening. The wall of the dorsal duct is a layer of squamous cells, each possessing a conspicuous nucleus, just as in excretory tubes, but never made of pavement cells as in the blood vessels. Near its posterior end there is a circular (sphincter) muscle. In the lumen of the dorsal duct there are always to be found mature sperm cells, and, moreover, the spermatozoa have been seen moving from the testes into the dorsal duct. Furthermore, even in mature testes there is no trace of direct communication to the outside through an external pore, and the dorsal duct has been found only in males. Therefore, I think that the dorsal duct is a unique sperm duct in this particular species. It is entirely new, being unknown among the hitherto known nemerteans. The presence of spermatozoa in the dorsal duct, which I mentioned previously, may be due to the contraction of the body of the worm, in which the testes had become broken and their contents thrown into the dorsal duct. But that such a special duct 'is present in connection with the digestive tube is certainly noteworthy. With what organs of other species this dorsal duct is homologous is not clear, because I have not studied the development of the worm, but, based upon anatomical observation, there might be some relation between the presence of the dorsal duct and the shortness of the proboscis sac. The proboscis sac in the male has a very small posterior chamber, and behind that it becomes a bundle of fibers directed slightly dorsally and reaching the inner surface of the longitudinal muscle layer. Then gradually little spaces develop in that bundle of fibers, and further along it is clearly surrounded by a cellular wall, thus becoming the dorsal duct. In the female it is the same as far as the point where the structure comes in contact with the longitudinal muscle layer, but then

there is no recognizable structure beyond that point. Therefore the so-called dorsal duct mentioned here is the proboscis sac, which has been suddenly pinched off behind the proboscis. Thus there are two parts to the proboscis, anterior and posterior. In the males the anterior region is short and a true proboscis sac, while the posterior part becomes finally connected with the posterior end of the intestine. Thus it serves as a sperm duct in this sex, while in the female the posterior part has degenerated completely.

There is no sensory cerebral organ.

From what is known about the two species of this genus the young worms are attached to the gills of the host and suck its blood. When they become mature they enter the egg mass and there become sexually ripe and deposit their eggs in mucous tubes. After segmentation the larvae develop, leave the egg shell, and stay among the crab eggs or inside the tube. As the worms develop they molt and assume the usual form, creeping on the body surface of the host and reaching its gills, where they live until the next year. Therefore the worms found on the egg masses are always without exception mature.

The specimens I collected were all mature ones, because none were found on the gills. This Japanese species probably has the same life cycle as foreign species, but on this I cannot be positive. The host crab, *Eriocheir japonicus*, lives only in fresh or brackish water. At the time of this collection (1906) there was a heavy rainfall and flood, which carried the crabs down to the bay into brackish water. I never found the worms again, although I searched repeatedly. The crab lives in Yokohama Bay, where the salt concentration is high, as well as in fresher waters. I became curious whether the fresh water crabs are parasitized with this nemertean but unfortunately none were collected up to the present time.

Comparison of the new species with the known species: (1) the lateral nerve trunk goes around the ventral side of the posterior end of the intestine, instead of around the dorsal side as in other species; (2) the anterior commissure of the lateral blood vessels is located far behind the usual point; (3) a special dorsal vessel, present in males only, is entirely different from other species.

Therefore I propose to name this species *mitsukurii*, not only in honor, but in commemoration of Professor Mitsukuri.

GEOGRAPHICAL DISTRIBUTION AND HOSTS

Many specimens of nemerteans which the writer believes should be, for the time being at least, referred to as *Carcinonemertes mitsukurii* Takakura were collected from the egg masses of several crabs in the collections of the Museum of Comparative Zoology and the United States National Museum. These are shown in Table 16. A few measurements of those specimens which were cut in such planes as to facilitate accurate measurement are included.

All the crab hosts shown in Table 16 belong to the Portunidae. In most respects the worms agree with Takakura's description. The basis, however, is slightly shorter. The writer is unable to state whether this difference is significant. It may be that the basis in this species is variable in size over a range wide enough to include the above measurements. It is impossible to determine from the sectioned material whether the anal commissure of the lateral nerves passes above or below the posterior end of the intestine. The posterior proboscis chamber in all these worms is short and thick, and about twice as long as wide, corresponding to

TABLE 16.—DISTRIBUTION RECORDS OF *Carcinonemertes mitsukurii* BASED ON
MUSEUM MATERIAL

Name of Host	Locality and Date	Length (mm)	Diameter (mm)	Basis (μ)	Stylet (μ)
Charybdis miles de Haan USNM 50792..........	San Andreas I., between Marinduque and Luzon, P. I., 1908	2.2 2.7	0.13 0.14	22.5 x 7.0	... ...
Charybdis cruciata USNM 2112 (Herbst)...	Hong Kong, China	3.5	0.28	20.5 x 7.0	...
Charybdis erythrodactyla MCZ 5337 (Lamarck)...	Kauai, Hawaiian Is.		badly disintegrated		
Charybdis erythrodactyla MCZ 636 (Lamarck)....	Apiang, Kingsmills Is., 1860	5.5	0.24	20.5 x 5.0	...
Charybdis erythrodactyla MCZ 5339 (Lamarck)...	Society Islands	16.0 1.4	0.60 0.11	.... 21.0 x 8.0	... ...
Charybdis erythrodactyla USNM 29654 (Lamarck)	Honolulu market	5.6 5.0	0.31 0.22	21.0 x 6.5 22.5 x 7.0	8.5 .
Portunus pelagicus MCZ 1638 (Linnaeus)...	Singapore		badly disintegrated		

mitsukurii. There are cephalic muscle fibers around the rhynchodaeum (fig. 9), as in other species of the genus. The shape of the basis is shown in fig. 29. Sketches of the mucous sheaths of this species are found in figs. 1, 3, and 41.

A comparison of the three points which Takakura considered diagnostic characters for his species with the situation found in *C. c. imminuta* and other species in the genus will show that all three of the items can no longer be held diagnostic of *mitsukurii* alone. The anal nerve commissure is ventral in both *imminuta* and *mitsukurii*, the anterior blood vessel commissure in both is located immediately in front of the brain, and in both species there is found the unique type of male reproductive system, referred to by the writer as Takakura's duct. One clear difference between the two species seems to be the fact that in *mitsukurii* the anal blood vessel commissure crosses dorsally to the posterior end of the intestine, while in *imminuta* it crosses ventrally to it. As for other diagnostic features of *mitsukurii*, little can be stated with certainty. Accord-

ing to Takakura (1910), there is a pair of caeca from the dorsal side of the stomach reaching near the brain. It must remain for future investigations, involving the comparative study of live and properly fixed material from various regions, to decide whether *C. mitsukurii* shall stand as a distinct species or shall be placed in synonymy with *C. carcinophila*. In the meantime the writer feels that it is best to consider all these worms from the western and central Pacific Ocean as belonging to *C. mitsukurii*. Such a treatment may avoid taxonomic confusion later on.

CARCINONEMERTES COEI SP. NOV.

SIX SPECIMENS of a hitherto unknown nemertean belonging to the genus Carcinonemertes were found on the egg mass of a single female specimen of *Charybdis natator* (Herbst), no. 5341 in the collection of the Museum of Comparative Zoology at Cambridge, Massachusetts. The crab, which belongs to the family Portunidae, had been collected at Zanzibar, on the east coast of Africa, in 1862. One of the worms sectioned very unsatisfactorily. The other five specimens, two males and three females, were successfully cut into serial sections 10 μ thick. Considerable difficulties were encountered because of the mucous sheaths surrounding the worms and because of the poor fixation (probably in 70 to 80 per cent alcohol). Four of the serial sections were stained with safranin and fast green. The fifth was stained with Heidenhain's iron haematoxylin. All the worms were in separate sheaths, except two, a male and a female, which were in the same sheath.

Although, like the other species of the genus, the characteristics by which this species can be distinguished from related species are small, nevertheless there are a few fundamental differences between each of the known species and the new worm. The writer proposes to name the new species *Carcinonemertes coei*, in honor of Dr. W. R. Coe. The diagnosis of the species is as follows:

Carcinonemertes coei sp. nov.

Genus Carcinonemertes. Body stout (fig. 23), with both ends rounded, and of about the same diameter throughout. Average length 6 mm, average diameter 0.5 mm, about 10 times longer than wide in preserved specimens. Head not demarcated from body. No lateral grooves or cerebral sense organs.

Mucous sheath (fig. 35) several millimeters longer than body. Lapilli on surface of sheath small, about 140 by 90 μ, light brown in color and widely scattered. Lapilli not all of same shape, but some elongated and poorly delimited.

Color in preserved specimens yellowish white. Single pair of ocelli, slightly irregular in shape, very dark brown or black, about 27 μ in

diameter, located 160 μ apart at a level 145 μ behind the anterior tip of the body (fig. 35).

Proboscis much reduced in size. Anterior chamber thin-walled and narrow. Basis (fig. 4) 22.7 μ in length, swollen posteriorly. Posterior diameter 7.5 μ, anterior diameter 3.7 μ, posterior end being twice as large as anterior end. Basis stains heavily with safranin and with Heidenhain's iron haematoxylin, as in other species. Basis surrounded at least in its posterior two-thirds by a single layer of cells. Stylet (fig. 4) slender, 8.7 μ long, or about ⅓ to ½ as long as the basis. Ratio of stylet to basis 0.382. Gland cells associated with stylet apparatus bunched posteriorly, near posterior end of basis. Middle proboscis chamber highly muscular, fibers running in various directions. Size of middle chamber 33 by 28 μ, slightly longer than its diameter, situated posteriorly to basis with its anterior half enclosed by the enlarged glandular tissue associated with the basis and stylet. Posterior chamber of proboscis non-muscular, glandular, thick-walled, situated immediately posteriorly to the middle chamber and in approximately the same plane as the preceding part of the proboscis. Size 78 by 47 μ, longer than wide.

Esophagus large and muscular as in other species of genus. Alimentary canal straight and presenting few peculiarities, other than the reduction in size of the lateral pouches because of the enormous development of the ovaries.

Nervous system as in other species of genus.

Cephalic glands, submuscular glands, outer epithelium, circular and longitudinal muscle layers, and cephalic muscle fibers similar to those in other species.

Testes numerous, scattered through the region between submuscular glands and intestine. Takakura's duct present.

Ovaries very numerous. In sections an inner and an outer row on each side of the intestine (fig. 33), making four rows in all. Outer row situated close to submuscular glands, inner row located deeper in the body adjacent to the intestine. Ovaries in the two rows alternate with some, but not absolute, regularity. Each ovary with several developing eggs. Intestinal pouches apparently much reduced in size, the space between the submuscular glands and the.intestine being almost wholly occupied by the ovaries. (Fixation was so poor that it was virtually impossible to distinguish the intestinal pouches.) In sections, three-fourths of the diameter of the body is made up of ovaries, which extend from the anterior end of the intestine to the posterior end of the body.

This species differs from known species in having a much stouter body (compare figs. 22 and 23), the basis being swollen posteriorly (compare fig. 4 with figs. 27, 28, 29, 30, and 31), and there being two rows of ovaries on either side of the intestine (compare figs. 26 and 33).·

At present *Carcinonemertes coei* is known only from the egg mass

TABLE 17.—MEASUREMENTS OF *Carcinonemertes coei* SP. NOV.

Sex	Length (mm)	Diameter (mm)	Length of Basis (μ)	Diameter of Basis (μ)	Stylet Length (μ)	S:B Ratio	Middle Chamber (μ)	Posterior Chamber (μ)
Male.......	4.2	0.5	...	8.4–4.2	..	.....	30 x 20	63 x 28
Female.....	5.8	0 6	...	6.3–4.2	..	.....	35 x 31	84 x 68
Female.....	6.0	0.7	21	6.0–2.5	8	0.381	38 x 31	108 x 70
Female.....	8.0	0.4	24	8.4–3.5	9	0.375	25 x 38	62 x 35
Male.......	...	...	23	7.5–4.0	9	0.391	35 x 19	73 x 35
Averages...	6.0	0.5	22.7	7.5–3.7	8.7	0.382	33 x 28	78 x 47

of a single specimen of *Charybdis natator* (Herbst) mentioned above. The holotype and four paratypes have been deposited in the Museum of Comparative Zoology at Cambridge, Massachusetts.

Table 17 shows the individual measurements of the five specimens upon which the preceding description is based.

THE FAMILY ASSIGNMENT OF THE GENUS

THE GENERA OF THE EMPLECTONEMATIDAE

THE HOPLONEMERTEAN suborder Monostilifera was divided by Böhmig (1933) into two tribes, the Archimonostilifera, in which the mouth and proboscis open separately, and the Eumonostilifera, in which the mouth and proboscis have a common opening. To the latter tribe belongs the family Emplectonematidae Bürger (1904), in which the genus Carcino-nemertes has been placed by most modern writers. Böhmig (1933) char-acterized the family as having long, flat, thread-like bodies, short and relatively thick proboscides, very much reduced or absent cerebral organs which lie in front of the brain, few eyes (often 4, 2, or 0), and being of separate sexes.

Five genera were listed by Böhmig (1933) in this family, but since that time five other genera have been described which in the writer's opinion belong in or near this family. The ten genera are as follows:

Emplectonema (Stimson, 1857, p. 163)
Paranemertes (Coe, 1901, p. 32)
Nemertopsis (Burger, 1895, p. 548)
Gononemertes (Bergendal, 1900, pp. 313-328)
Carcinonemertes (Coe, 1902b, pp. 409-411)

Arenonemertes (Friedrich, 1933, p. 504)
Nemertellina (Friedrich, 1935, p. 10)
Nemertellopsis (Friedrich, 1935, p. 12)
Atyponemertes (Friedrich, 1938, p. 22)
Dichonemertes (Coe, 1938, p. 221)

The two genera Gononemertes and Carcinonemertes appear to be more closely related to each other than to the rest of the genera. Gonone-

mertes has no stylet apparatus and Carcinonemertes has only one central stylet. The other genera have the central stylet and in addition one or two pairs of accessory stylet pouches.

Diagnosis of the Carcinonemertidae

The first and only use of the name Carcinonemertidae, in so far as the writer is aware, is that of Sumner, Osburn, and Cole (1913). In their list of the fauna of Woods Hole and vicinity (p. 591), they listed *Carcinonemertes carcinophila* (Kölliker) as follows:

Family Carcinonemertidae

Carcinonemertes carcinophila (Kölliker)
Coe, 1902, 441.
Nobska Point, Katama Bay, Nememsha Bight.
"Parasitic on the gills of various species of crabs when young, migrating to the egg masses of the crab at the approach of sexual maturity." Locally reported only from the "lady crab" (*Ovalipes ocellatus*). In the case of a large number of crabs of this species examined by Dr. Coe during July and August of various years the parasites were found on the gills of about 10 per cent of the female crabs, but none were found on the males.

No diagnosis or description of the new family Carcinonemertidae was given, nor was the name Carcinonemertidae designated as a new family name. No indication of the genera and species to be included in the family was given, other than the mention of *C. carcinophila*.

There is nothing in the International Rules of Zoological Nomenclature which governs the proposing of new family names, except that they must end in -idae, must be founded upon the type genus, and must be uninomial. The name Carcinonemertidae, therefore, is a valid name.

A brief diagnosis of the family Carcinonemertidae (Sumner, Osburn, and Cole, 1913) is as follows:

Monostiliferan hoplonemerteans living as ectohabitants on the gills and egg masses of crabs. One central stylet, no accessory stylet pouches or accessory stylets. Proboscis very short, reaching scarcely beyond the posterior end of the muscular part of the esophagus. Anterior chamber of the proboscis extremely short and non-glandular. Lateral nerves lie internal to the massively developed submuscular glands. Cephalic glands well developed. No cerebral sense organs.. Cephalic muscle fibers present. Excretory apparatus apparently absent. Dorsal blood vessel absent. Takakura's duct present in males. Internal fertilization and viviparity commonly occur. Excessive development of eggs and spermatozoa. Mucous sheaths secreted, attached to abdominal endopodite hairs of ovigerous crabs.

The family includes one genus, Carcinonemertes, with four species, *C. carcinophila carcinophila* (Kölliker), *C. carcinophila imminuta* described above, *C. epialti* Coe, *C. mitsukurii* Takakura, and *C. coei* also described above.

The family Carcinonemertidae may be distinguished from the most closely related family, the Emplectonematidae, by the following characteristics: (1) members live as ectohabitants of crabs; (2) one central stylet, no traces of accessory pouches or stylets; (3) no cerebral organ; (4) Takakura's duct in males; (5) massive development of both cephalic and submuscular glands.

The adoption of the family Carcinonemertidae leaves the other nine genera in the family Emplectonematidae. Of these Gononemertes is outstanding and probably will not remain in that group when more is known about its anatomy and development.

As Coe (1902a) has stated, the members of the genus Carcinonemertes appear to be more modified in relation to their dependent way of life than Gononemertes, although they still retain ocelli and a central stylet in the proboscis.

KEY TO SPECIES

It should be apparent that the use of a key alone for identification of an unknown worm in this genus would be unwise. The investigator should have the most detailed descriptions at hand, together with not only one but if possible several specimens of the unknown worm, preferably of both sexes. Measurements made while the animals are alive are of great help in identification. The following key may serve as a preliminary aid in identification of species of the genus Carcinonemertes.

1. Ovaries in two rows on each side of the intestine, an inner and an outer row; basis twice as large in diameter posteriorly..................*C. coei*
   Ovaries in a single row on each side of intestine; basis nearly cylindrical....2
2. Posterior proboscis chamber bent dorsally at an angle to the proboscis; body less than 6 mm long......................................*C. epialti*
   Posterior proboscis chamber not bent at an angle but in same plane as preceding part of proboscis; body may be less than 6 mm long, but usually more, reaching up to 70 mm......................................3
3. Anal blood vessel commissure dorsal to posterior end of intestine..*C. mitsukurii*
   Anal blood vessel commissure ventral to posterior end of intestine............4
4. Basis may be as short as 19 μ, usually from 25 to 30 μ in length, diameter 6 to 8 μ; stylet 8 to 12 μ in length; body 20 to 70 mm in length ....*C. c. carcinophila*
   Basis ranges in length from 19 to 23 μ, averaging 21 μ, diameter 4.5 to 6 μ; stylet 6 to 9.5 μ, averaging 7.4 μ; body 0.4 to 35 mm in length, averaging about 10 to 25 mm................................*C. c. imminuta*

SIGNIFICANCE OF TAKAKURA'S DUCT

The reproductive system in the Nemertea is very simple in structure. The gonads in both sexes are usually placed alternately with the intestinal pouches. In some genera, however, i.e, Carcinonemertes males, Gonone-

mertes, Tubulanus, and Malacobdella, they are extraordinarily numerous and do not alternate regularly with the pouches of the gut.

Each gonad empties to the outside through an individual duct. In the case of Zygeupolia, described in detail by Thompson (1901, p. 713), the testis is a simple sac, with a single duct, opening on the dorsal surface of the body near the side of the rhynchocoel. The duct passes through the longitudinal and circular muscle layers, expands into a small bulb, and then opens to the exterior through the integumental epithelium. The ovaries do not have preformed ducts; the eggs are discharged by the rupture of the body wall.

Böhmig (1933, p. 53) stated, regarding the gonads of the Nemertea, that "ihre einfachen Ausführgänge münden zumeist auf dem Rücken oder an den Seitenflächen in einer oder in mehreren Reihen ange-ordnet nach aussen, seltener sind sie gegen die ventrale Körperfläche verschoben."

In some of the pelagic nemerteans, especially Nectonemertes and Phallonemertes, Coe (1926) described testes which in some respects remind one of the condition described above in Carcinonemertes. Each testis, located in the cephalic region, is retort-shaped, with its neck pointed ventrally and laterally. The body of the retort contains the germinal cells. The neck is marked off from the body of the gonad by a constriction, distal to which the neck then expands into a spacious chamber, whose wall is non-germinal and is provided with a few longitu-dinal muscle fibers. In this chamber (the seminal vesicle) the ripe spermatozoa collect prior to being discharged through a short sperm duct to the opening on the genital papilla. The opening of the seminal vesicle to the exterior appears to remain closed except when the bundles of spermatozoa are discharged.

The gonad is not always a simple sac. Friedrich (1939, p. 238) has described in *Amphiporella baltica* Friedrich a double-sacked gonad, with ventral and dorsal parts, opening in a common pore laterally. The same condition is present also in *Amphiporus bürgeri* Isler, according to Friedrich.

Secondary sexual characters are present only in members of the Polystilifera pelagica, all of which are pelagic nemerteans. In Necto-nemertes, Balaenanemertes, and Parabalaenanemertes the testes open to the exterior on small papillae. In *Phallonemertes murrayi* Brinkmann the papillae are extended as slender penes, which, according to Brinkmann (1917, pp. 62-63), may be inserted into the oviducts of the female where their tips, stuffed with spermatozoa by the contraction of the muscula-ture of the spermary, may break off. The genital papilla may thus serve as a spermatophore.

In so far as the writer is aware, no important variations from the typical sac-like testes with their single ducts to the exterior, other than those just mentioned, have been discovered in the phylum Nemertea. The translation of Takakura's work on *C. mitsukurii*, together with the writer's independent observations on *C. c. imminuta* and other species, brings to light a hitherto generally unrecognized type of male reproductive system in the males of Carcinonemertes. This has been referred to above as Takakura's duct.

The Nemertea have been derived phylogenetically by Reisinger (1933, p. 33) from the Acoela. Schepotieff (1912), using emulsions of Cerebratulus lacteus (a nemertean), Prostherceraeus (a turbellarian), and Capitella (an annelid), found that the Wassermann's reaction is positive between Nemertea and Turbellaria and negative between Nemertea and Annelida, indicating that the Nemertea are more closely related to the Turbellaria than to the Annelida. Bürger (1897-1907, p. 472) concluded also that the Nemertea probably arose from an ancestral stock of the Turbellaria, probably possessing simple reproductive organs. In the evolution of the modern Turbellaria the reproductive system has undergone many complications, while in the Nemertea it has remained very simple. The presence of Takakura's duct indicates that the male system is not always as simple as Bürger believed, however.

Bürger (1897-1907) derived from the Protonemertini (Palaeonemertea) two main lines, the Heteronemertini (Heteronemertea) and the Mesonemertini (Palaeonemertea in part). From the Mesonemertini he derived the Metanemertini (Hoplonemertea). The genus Emplectonema was placed as the most primitive of the Hoplonemertea and gave rise to the genus Carcinonemertes.

It is impossible to determine whether Takakura's duct is a structure carried over from some acoelan ancestor or whether it is a new structure. The duct somewhat resembles one of the paired male genital ducts found in the Acoela (von Graff, 1908, pp. 1950-1953, Pl. I, fig. 10, Pl. II, fig. 2). These ducts in the Acoela are paired and empty into a single median chamber provided with copulatory apparatus. The male genital opening is not associated with the alimentary canal. Since the primitive nemerteans have simple sac-like gonads with short, individual ducts leading directly to the exterior, and since Carcinonemertes is a rather advanced genus, being armed with a stylet and having nerves located well inside all the muscle layers of the body wall, it seems best to the writer to consider the condition of the male reproductive system in Carcinonemertes as a separate development, independent of possible acoelan ancestry. The hypothesis will be tested when the embryology of Takakura's duct is known. It is interesting to note that such an arrange-

ment, whereby the sperm duct empties into the alimentary canal, in reality forming a cloaca, is elsewhere present only in the Nemathelminthes and Tardigrada, unless the vitello-intestinal canal of some Trematoda be included.

RELATIONSHIPS TO HOST CRABS

NEARLY ALL the worms at Grand Isle taken from brown egg masses contained, as mentioned above, dark brown or black particles in their intestines (fig. 47). These resembled roughly the eyes and chromatophores of the crab embryos in their size, shape, and color. Such particles were not found in worms taken from yellow or orange egg masses, in which the crab embryos had not yet developed pigmented eyes or chromatophores, nor were they found in worms from the gills. It has already been stated that the nemerteans are able to evert the posterior muscular part of the esophagus. Its movements when thrust out of the body consist of strong peristaltic contractions, originating anteriorly. The diameters of the esophagi of 10 adult worms averaged 97 μ, with a maximum of 170 μ and a minimum of 41 μ. The eggs of *Callinectes sapidus* measure approximately 245 μ in diameter. It thus seems impossible that the esophagus can surround the eggs. But by constant sucking and pressing motions of the esophagus the worm may be able to rupture eventually the egg membranes and draw out the soft parts of the embryonic crab within.

In a serial section of *C. c. imminuta* from *Callinectes marginatus* (Milne-Edw.) collected at St. Thomas, West Indies, in 1871, the writer has seen in the intestine many dark particles similar to those mentioned above in *C. c. imminuta* from Grand Isle. Of more significance, however, is the fact that several setae and the delicate chitinous covering of the prezoea can be seen, indicating that the worms are capable of feeding upon the crab embryos.

Van Beneden (1876) believed that the European *C. carcinophila* fed upon dead or disintegrating embryos of the crab host. But because of the rarity of such eggs and the great abundance of worms on any one egg mass it seems more probable that the nemerteans feed upon the living crab embryos also. Churchill (1919, p. 97) estimated that in an egg mass of the usual size there are from 1,700,000 to 2,000,000 eggs. The number of eggs eaten by the nemerteans even in extremely heavy infestations would probably be negligible.

It has been indicated above that growth apparently occurs while the worms are on the gills of the crab. The nature of the food necessary for such growth and the mechanism of obtaining it are uncertain. Coe

(1902a) suggested that the worms are able to evert the proboscis and puncture the gills with the stylet, thereafter drawing in blood from the wound by pumping motions of the esophagus. However, the writer has found no evidence for the eversion of the proboscis. The blood corpuscles of *C. sapidus,* figured by Howell (1886, Pl. XVII, figs. 6-8), are of sufficiently small size to be taken in by the nemerteans. The question whether the worms puncture the gills and feed upon the blood of the crab must remain unsettled until the actual process is observed, or until the worms can be made to ingest colored substances injected into the crab's blood which will not pass through the chitinous gill covering of their own accord. No injuries to the gills made by the nemerteans were seen by the writer.

If the worms feed only upon the eggs of the crabs then there is a long period of time between the times when the crab is ovigerous when the nemerteans go without food. The worms are sexually mature only on the egg masses, where food is abundant. When on the gills, the gonads are undeveloped or rudimentary. In starvation experiments with various turbellarians it has been observed that the reproductive organs are the first to disappear. Perhaps a similar situation exists in Carcinonemertes.

The writer was able to maintain specimens of Carcinonemertes from the gills of a crab alive in a finger bowl of clean sea water, changed once every day, for over two months. No observable modifications in internal structure were present at the end of that time. A similar ability to withstand separation from the normal host and food has been found by Riches (1893-1895, p. 22) in the commensal genus Malacobdella. Carcinonemertes is probably able to last over the winter months between the ovigerous states of the crab host without food. The worms coil up in their cyst-like capsules between the gill lamellae and remain quiescent. The water during the winter months is cooler, with the crabs migrating to greater depths, and the worms do not require as much food as in the summer months when the crabs frequent the warmer and more shallow waters.

No injuries to the gills, even in heavy infestations, were found, but a heavy infestation is, however, probably detrimental because the free flow of water between many of the lamellae is prevented. By a modification of the method of Damant (1920) the area of an average sized gill lamella was found to be about 56.8 square millimeters on each side of the median raphe. Three nemertean capsules were present on one side of the lamella, which measured in area 6.28, 7.80, and 4.11 square millimeters respectively, or a total capsule area of 18.19 square millimeters. Thus nearly one-third of the area of one side of the lamella was occupied by the worm capsules and obstructed from the free flow of water. In heavy infestations nemerteans are present between approximately every second

gill lamella, and the amount of interference with flow of water becomes considerable. From all appearances, however, the heavily infested crabs are just as vigorous as the uninfested ones. An attempt was made to determine experimentally the effects of the nemerteans, using a modification of the method employed by Keys (1928) with fish parasitized by isopods, in which the effect of the parasites was measured by their influence upon the death rate in various semilethal environments. However, the inadequate laboratory equipment at hand was not capable of producing trustworthy results. Hay and Shore (1918) have suggested that when the gill chambers become heavily infested with the barnacle *Octolasmis mülleri* the crab is doubtless weakened and made an easy victim for fish or storms.

Dieck (1874) in describing his *Cephalothrix galatheae* (? = *C. carcinophila*) wrote:

Ist der Eiervorrath verzehrt, so ziehen sich die Thiere in die Kiemenhöhle des Krebses zurück, um da wahrscheinlich ihren Ectoparasitismus in veränderter Art fortzusetzen, indem sie die zarte Membran der Kiemen anbohren und so zum Blute des Thieres gelangen. Wenigstens fand ich nicht nur häufig die Kiemenhöhlen von Würmern bewohnt, sondern sah, auch beim Zerzupfen derselben aus dem Innern Blutzellen ausströmen, welche sich in nichts von denen der Galathea unterschieden und wahrscheinlich, weil kurz vorher verschluckt, noch unverdaut geblieben waren.

From the existing evidence the writer takes the view that the members of the genus Carcinonemertes are not true parasites but ectohabitants, which feed upon the eggs of the crab.

MODIFICATIONS COINCIDENT WITH ECTOHABITATION

IN THE members of the genus Carcinonemertes there is excessive development of the cephalic and submuscular glands. By means of the abundant mucus the worms are enabled to adhere to the body of the host. With the mucus they form their capsule walls when living on the gills and their tough, elastic sheaths while on the egg masses.

Complicated sense organs on the head, such as are present in many nemerteans, are absent in these worms which live a sheltered life on the body of the crab.

The posterior part of the esophagus is modified into a large, muscular chamber which by its peristaltic pumping action draws food into the body.

The proboscis is very much reduced and immobile. The chief functions of the proboscis in other nemerteans are food-getting and burrowing. Apparently since abundant food is everywhere present (when the worms are living on the egg masses at least), the proboscis has become atrophied and is non-eversible.

The number of gonads in relation to body size is large. The testes are especially numerous. Internal fertilization and viviparity protect the

developing young for a longer time than would be the case if there were external fertilization only. The chances for each fertilized egg to reach maturity are thus increased.

HOST DISTRIBUTION AND FREQUENCE ON PORTUNIDAE

A TOTAL of 334 ovigerous crabs was examined at the Museum of Comparative Zoology and at the United States National Museum. These included representatives of nearly all the large and commonly found families, except those which are terrestrial or fresh-water in habitat. Table 18 summarizes the results of the examination for Carcinonemertes.

Several hosts for the genus Carcinonemertes outside the family Portunidae have been reported. The complete list of non-portunid infestations is shown in Table 19.

A complete list of all the species of Portunidae now known to be infested with members of the genus Carcinonemertes is given in Table 20.

In all there are 27 species and subspecies of Brachyura (and probably one species of Anomura) known to be infested with Carcinonemertes. These nemerteans infest only those crabs with suitable ecological habits. According to Gerstaecker and Ortmann (1901, p. 1182), there are five ecological zones in which the Brachyura (and the Decapoda in general) live. They are the continental, fluvial, littoral, pelagic, and abyssal zones.

TABLE 18.—SUMMARY OF HOSTS EXAMINED AND INFESTATION FOUND IN MUSEUM MATERIAL

Family	Number of Species Examined	Number of Specimens Examined	Number Infested with Carcinonemertes
Euryalidae	1	1	...
Portunidae	53	204	29
Xanthidae	18	37	...
Majidae	22	41	...
Grapsidae	11	27	...
Dromiidae	2	2	...
Leucosiidae	2	2	...
Calappidae	5	6	...
Cancridae	3	6	...
Gecarcinidae	2	2	...
Goneplacidae	1	3	...
Galatheidae*	1	3	...
Totals	121	334	29

*This family belongs to the Anomura; the rest are Brachyura.

TABLE 19.—RECORDS OF INFESTATIONS BY CARCINONEMERTES OUTSIDE THE
FAMILY PORTUNIDAE

Host	Family	Species	Author
Galathea strigosa Linnaeus....	Galatheidae	?*C. c. carcinophila*	Dieck, 1874
Xantho floridus Mont.........	Xanthidae	*C. c. carcinophila*	Giard, 1888
Pugettia producta (Randall)...	Majidae	*C. epialti*	Coe, 1902a
Eriocheir japonicus de Haan...	Grapsidae	*C. mitsukurii*	Takakura, 1910
Hepatus epheliticus (Linnaeus)	Calappidae	*C. c. imminuta*	Humes
Persephona punctata aquilonaris Rathbun.....	Leucosiidae	*C. c. imminuta*	Humes
Panopeus herbstii (Milne-Edwards)...............	Xanthidae	*C. c. imminuta*	Humes
Menippe mercenaria (Say)....	Xanthidae	*C. c. imminuta*	Humes

TABLE 20.—RECORDS OF INFESTATIONS BY CARCINONEMERTES IN THE
FAMILY PORTUNIDAE

Host Crab	Species	Author
Carcinides maenas (Linnaeus).......	*C. c. carcinophila*	Van Beneden, 1861; McIntosh, 1869 and 1873-1874; Giard, 1888 and 1890; Joubin, 1890
Callinectes sapidus Rathbun........	*C. c. carcinophila*	Coker, 1901; De Turk, unpublished
	C. c. imminuta	Humes
Callinectes ornatus Ordway........	*C. c. carcinophila*	De Turk, unpublished
	C. c. imminuta	Humes
Bathynectes superba (Costa)........	*C. c. imminuta*	Pearse, unpublished
Portunus spinimanus Latreille......	*C. c. carcinophila*	De Turk, unpublished
Ovalipes ocellatus ocellatus (Herbst)..	*C. c. carcinophila*	Coe, 1902a; Sumner, Osburn, and Cole, 1913; De Turk, unpublished; Humes
Ovalipes ocellatus guadulpensis (Saussure)....................	*C. c. carcinophila*	De Turk, unpublished
Portunus sayi (Gibbes).............	*C. c. imminuta*	Humes
Arenaeus cribrarius (Lamarck)......	*C. c. imminuta*	Humes
Portunus spinicarpus (Stimpson)....	*C. c. imminuta*	Humes
Callinectes bocourti M.-Edw........	*C. c. imminuta*	Humes
Callinectes marginatus M.-Edw......	*C. c. imminuta*	Humes
Cronius ruber (Lamarck)...........	*C. c. imminuta*	Humes
Callinectes danae Smith...........	*C. c. imminuta*	Humes
Euphylax dovii Stimpson...........	*C. epialti*	Humes
Charybdis miles de Haan...........	*C. mitsukurii*	Humes
Charybdis cruciata (Herbst)........	*C. mitsukurii*	Humes
Charybdis erythrodactyla (Lamarck)..	*C. mitsukurii*	Humes
Portunus pelagicus (Linnaeus)......	*C. mitsukurii*	Humes
Charybdis natator (Herbst)........	*C. coei*	Humes

Since Carcinonemertes will not live in air or fresh water, the crabs of the first two groups are eliminated as possible hosts. So far none of the abyssal crabs have been found infested. In such situations the crabs are not abundant enough and the conditions for transfer of the free-swimming larvae are unfavorable.

All of the species which have been thus far reported infested live in the littoral zone, with the possible exception of the one case reported above in the pelagic group, i.e., *Portunus sayi* (Gibbes), at Grand Isle, Louisiana. In that case, however, abnormal environmental factors brought about an infestation which was more or less accidental in character. For a month or more before the crab was collected offshore winds had been driving in great rafts of Sargassum or Gulf weed, upon which *P. sayi* lives. Much of this weed entered Barataria Bay through the passes and remained there for several weeks. On July 4, 1940, an adult female specimen of *P. sayi* was collected in Barataria Bay, just north of Grand Terre. One extremely minute specimen of *C. c. imminuta* was found on the gills. This worm, not exceeding 500 μ in length, was unfortunately lost. The writer believes that the presence of the worm on *P. sayi* was accidentally brought about by the unusually close contact between the latter and the numerous heavily infested *Callinectes sapidus,* which abounds everywhere in Barataria Bay and often crawls about in the Sargassum. All the specimens of *P. sayi* from other regions were uninfested.

All the infested crabs in Tables 19 and 20 live in depths less than 50 meters (i.e., they are omitted from Doflein's (1904, pp. 288-308) extensive list of Brachyura which live at depths greater than 50 meters or which in other words are deep-water species), with the exception of six species. These are *Xantho floridus* living at depths up to 77 meters, *Portunus spinimanus* to 97 meters, *Callinectes sapidus* to 143 meters, *Portunus spinicarpus* at 55 to 730 meters, *Portunus sayi* from the surface to 1084 meters, and *Bathynectes superba* from 100 to 1410 meters. All these six are littoral, however, in their distribution, and are rare at great depths.

Certain conditions in the life habits of the littoral Portunidae make these crabs ideal hosts for members of the genus Carcinonemertes. In the first place, the littoral portunid crabs never leave the water, a habit of great advantage to the nemerteans, which dry rapidly in air. Incidentally this probably explains the extremely few infestations of zanthid and grapsid crabs, many of which often go about temporarily on land. Secondly, the portunids often swim about in the water, coming to the surface frequently. The positively phototactic free-swimming nemertean larvae seek the surface in response to the brighter light there. Thus the crabs and nemertean larvae are brought together, and the infestations

are begun. The fact that the entire family Majidae, the spider crabs, is, except for one species, *Pugettia producta,* uninfested is probably to be explained on the basis that these crabs do not swim to the surface and are therefore not brought in contact with the free-swimming larvae. In the third place, the habit of the Portunidae of swimming about actively tends to distribute the nemerteans over a large area, an important element in the survival and propagation of any animal which is closely dependent upon another for its existence. The rather stationary lives, in comparison, lived by the other littoral families of crabs (Xanthidae, Grapsidae, Majidae, and others) may account in part for their being uninfested. Lastly, the portunid crabs live in shallow waters and often occur in great numbers, so that, by the restriction of space and the shorter distance from hosts to host, infestations of new and reinfestation of old hosts are facilitated.

The general conclusion to be drawn is that normally the members of the genus Carcinonemertes infest the littoral Portunidae. In each case in which these nemerteans have been found upon other hosts, special features of the environment probably have acted to bring about such infestations. At Grand Isle, Louisiana, the presence of nemerteans on *Panopeus herbstii, Menippe mercenaria, Hepatus epheliticus,* and *Persephona punctata aquilonaris,* all non-portunid crabs, is believed by the writer to be caused by the extreme abundance of infested *Callinectes sapidus* in that area and by the unusually favorable conditions for the crabs to come in contact with the free-swimming larvae. The fact that the infestations on non-portunid crabs are always very light indicates that opportunities for their infestation are not as great as in the portunid crabs. In the four non-portunid species infested at Grand Isle the infestation never exceeded five worms on any one crab, and these were all minute, though some were sexually mature. It is likely that throughout the geographical range of the genus unusually heavy infestations may occur in areas which, like the Barataria Bay region, have abundant and suitable crabs and favorable conditions for the transfer of the free-swimming larvae to the host crabs. Where such heavy infestations occur, it is also likely that light infestations of some of the common non-portunid crabs may occur.

There does not seem to be much host specificity in the genus Carcinonemertes. The host on which the nemertean lives is infested not because there is some particular and necessary thing about that host which excludes all other crabs as possible hosts, but because the habits of that crab and the habits of the nemertean larvae are so interrelated that under suitable environmental conditions infestation is made possible. Whatever species of aquatic crab can fit into the already established life history of the nemerteans that crab is potentially a host for the worms. The portunid crabs, of all the Brachyura, meet the nemertean requirements most ideally.
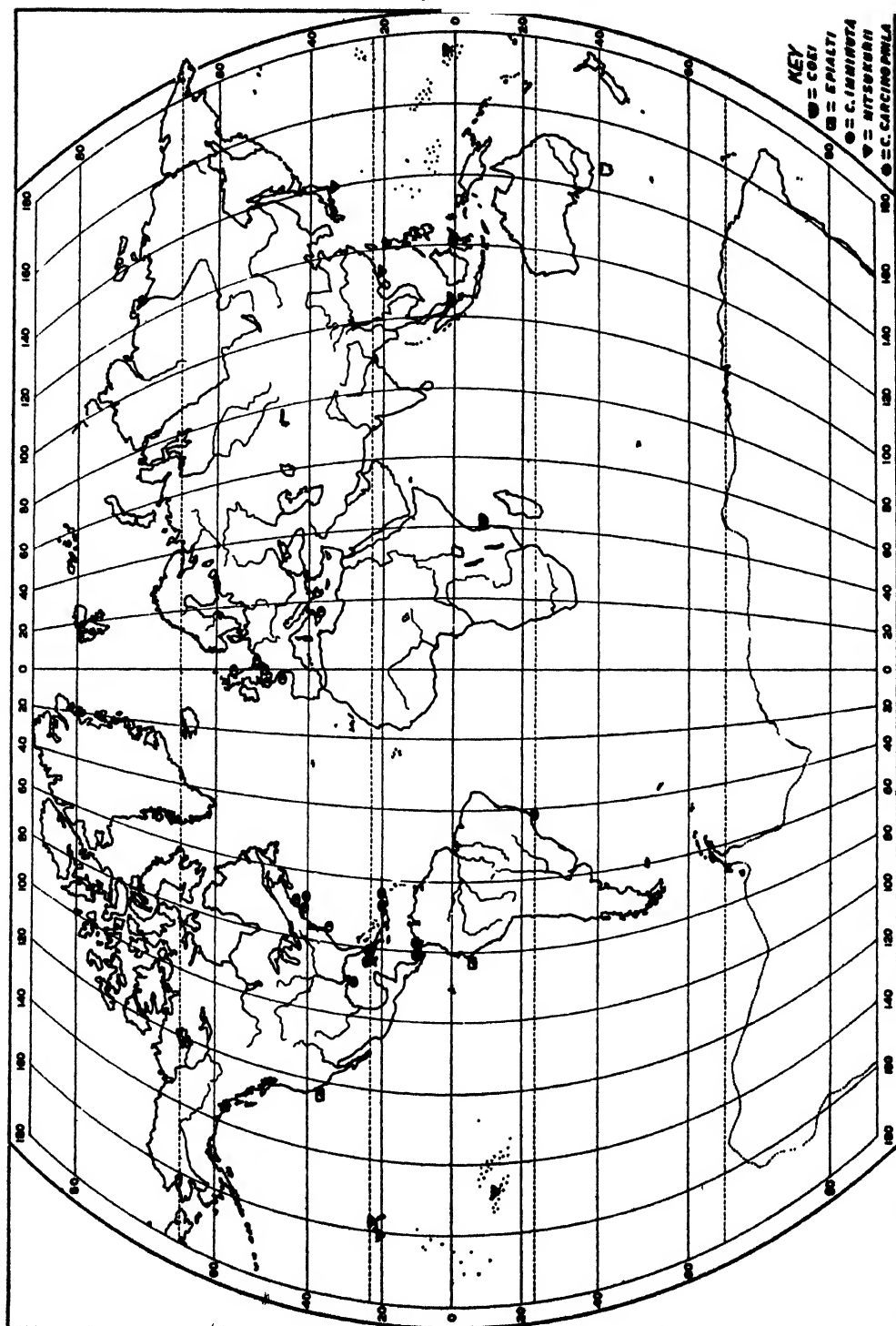
GEOGRAPHICAL DISTRIBUTION

THE MEMBERS of the genus Carcinonemertes are distributed in a wide belt around the earth between the tropic of Cancer and the tropic of Capricorn. The localities at which these nemerteans have been collected are shown on the map. The family Portunidae, on which the nemerteans chiefly occur, is of worldwide distribution in the littoral zone, and therefore offers opportunity for worldwide spread of the nemerteans.

Carcinonemertes carcinophila carcinophila (Kölliker) occurs at Messina, Sicily; Roscoff, Wimereux, and Concarneau, France; St. Andrews, Scotland; Ostende, Belgium; Beaufort, North Carolina; North Dennis and other regions south of Cape Cod, and Woods Hole, Massachusetts.

Carcinonemertes carcinophila imminuta has been found at Grand Isle, Louisiana; 10 to 20 miles south of the Tortugas, Florida; Fox Bay, Colon, Panama; Catano, San Juan Harbor, Puerto Rico; St. Thomas, West Indies, Porto Bello, Panama (Atlantic side); and Rio de Janeiro, Brazil.

Carcinonemertes epialti Coe is thus far known only from Monterey, California, and Payta, Peru.

Carcinonemertes mitsukurii Takakura has been collected at Yokohama Harbor, Japan; San Andreas Island, between Marinduque and Luzon, Philippine Islands; Hong Kong, China; Kauai, Hawaiian Islands; Apiang, Kingsmills Islands; Society Islands; Honolulu markets; and Singapore.

Carcinonemertes coei is thus far known only from Zanzibar, on the east coast of Africa.

SUMMARY AND CONCLUSIONS

(1) *Carcinonemertes carcinophila carcinophila* (Kölliker) is recorded, on the basis of data supplied by Dr. Wm. E. De Turk, from four new hosts and a new locality.

(2) A new variety, *Carcinonemertes carcinophila imminuta,* found at Grand Isle, Louisiana, differs from *C. c. carcinophila* in its smaller size, shorter and more slender basis, and shorter stylet. A distinct sexual dimorphism in size and color is present. These worms reach sexual maturity at sizes much smaller than any previously known mature nemerteans.

(3) These worms crawl but cannot swim, nor can they fragment the body. Crawling worms are negatively phototactic, but the free-swimming larvae are positively phototactic.

(4) On the crab gills the nemerteans form capsules by cementing the two adjacent gill lamellae together around themselves. All worms on the egg masses of the crab, except the very minute ones, live in mucous,

lapilliform sheaths which they secrete and in the branches of which the females deposit their eggs.

(5) Cephalic muscle fibers are present along the rhynchodaeum and around the brain and esophagus. The anterior non-muscular part of the esophagus is capable of complete eversion, bringing the posterior muscular part outside the body where it acts as a sucking and pumping organ.

(6) The intestine in adult females has deep lateral pouches, but in males and worms with undifferentiated gonads the pouches are very shallow or absent.

(7) The proboscis is incapable of eversion. The basis measures 21 by 5.3 μ, the stylet 7 μ in length, and the ratio of stylet to basis is 0.352.

(8) The anal blood vessel and nerve commissures are both ventral to the posterior end of the intestine.

(9) The male reproductive system consists of testes, vasa efferentia, a mid-dorsal vas deferens, and a seminal vesicle. These canals, referred to as Takakura's duct, carry the spermatozoa from the testes to the lumen of the posterior end of the intestine. A thick ridge of cells of unknown function projects centrally from the mid-dorsal body wall and accompanies that part of the vas deferens anterior to the seminal vesicle. A translation of Takakura's (1910) description of this system in *Carcino-nemertes mitsukurii* is presented.

(10) Early cleavage in *C. c. imminuta* is regular, equal, and probably of the spiral type. A ciliated free-swimming larva, slightly flattened dorso-ventrally, and bearing at each end a cirrus composed of several long, flagella-like elements, is formed.

(11) It is probable that the ciliated epithelium of the larva is not shed as claimed by earlier authors and that the only external change in the metamorphosis to a crawling worm is the loss of the cirri.

(12) The positive phototaxis of the larvae forces them to swim toward the surface where they come in contact with the crab host, *Callinectes sapidus*. Since immature crabs of both sexes and adult males molt relatively often, the nemerteans are unable to live long on them, being cast off at each ecdysis. Adult female crabs, however, do not molt, and this, together with the presence of eggs for food, makes infestation by nemerteans easy. The shallow water, comparative lack of strong currents, and the abundance of crabs all aid the larvae in coming in contact with new hosts in the Barataria Bay region.

(13) There is no correlation between the size of adult female crabs and infestation with nemerteans, or between the presence of nemerteans and the presence of the commensal barnacle *Octolasmis mülleri* (Coker).

(14) The worms migrate from the gills to the egg mass when the crab becomes ovigerous and back to the gills when the eggs of the crab

are hatched. Worms become sexually mature only on the egg masses of the crab. The gonads in worms on the gills are undeveloped. The nemerteans become sexually mature whenever the crab becomes ovigerous (in Louisiana from the last of March to the latter part of October). During cold weather, when the female crabs generally seek deeper water, the worms remain quiescent on the gills.

(15) The food of the nemerteans consists of the crab eggs. The effects of the worms on the crabs are slight. Free flow of water between the gill lamellae is prevented in heavy infestations, but heavily infested crabs appear to be just as vigorous as uninfested ones. No injuries to the gills were found, and it is improbable that the proboscis can be everted or that the stylet can pierce the chitinous covering of the gills.

(16) At Grand Isle, *C. c. imminuta* was found on eight species of crabs, six of them new host records for the genus. *Callinectes sapidus* is most commonly the host for these nemerteans in the Grand Isle region. On other crabs the nemerteans are small in size and few in number. Four other host crabs are reported from the West Indies and South America.

(17) A new host and locality for *Carcinonemertes epialti* Coe is reported.

(18) *Carcinonemertes mitsukurii* Takakura does not differ from *C. carcinophila* in the three respects that Takakura suggested, but does appear to differ in that the anal blood vessel commissure is dorsal instead of ventral to the posterior end of the intestine. Specimens which the writer believes should be temporarily at least assigned to *C. mitsukurii* were found on four new host crabs from new localities in the Pacific Ocean.

(19) A new species, *Carcinonemertes coei,* is described from *Charybdis natator* at Zanzibar. It differs from other species in its stouter body, the basis being swollen posteriorly, and having two rows of ovaries on each side of the intestine in the female.

(20) The family Carcinonemertidae, which name was first used by Sumner, Osburn, and Cole (1913), is re-established to include the single genus Carcinonemertes. The most important characteristics of the family are the presence of Takakura's duct, the much reduced proboscis with one central stylet and no accessory stylets or stylet pouches, the lack of cerebral sense organs, the massive development of the cephalic and submuscular glands, and the dependence upon crabs as a habitat. A key to the species and varieties is given.

(21) Although superficially the presence of Takakura's duct seems to indicate a relationship to the Acoela, the writer believes that this unique genital system is a separate development, independent of possible acoelan ancestry.

(22) The members of the genus Carcinonemertes are ectohabitants which feed upon the crab embryos, rather than ectoparasites.

(23) Of the 334 crabs examined in the collections of two museums, 29, all of them belonging to the family Portunidae, were infested with nemerteans. At the present time there are 26 species (one of which is divided into two subspecies) of Brachyura and 1 species of Anomura known to be infested with Carcinonemertes. Twenty out of the total of 27 brachyurans infested belong to the family Portunidae. Factors contributing to the high infestation of this family of crabs are (1) their wholly aquatic life, (2) their habit of swimming near the brightly lighted surface where the larvae of the nemerteans tend to collect, (3) their habit of swimming about actively, thus helping to distribute the worm larvae, and (4) their habit of living in shallow waters, often in great numbers, thus lessening the distance from host to host and increasing the chances· for transfer of infestations. There is no host specificity in these nemerteans. The genus Carcinonemertes is distributed in the littoral zone in temperate and tropical seas around the world.

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PLATES

All figures were drawn with the aid of a camera lucida, except figs. 5 and 51 which are free-hand sketches.

PLATE I

Fig. 1.—Mucous sheath of *C. mitsukurii* from egg mass of *Charybdis cruciata* at Hong Kong. Three crab eggs attached. Scale 1 mm.

Fig. 2.—Mucous sheath of *C. epialti* from egg mass of *Euphylax dovii* at Payta, Peru. Scale 0.5 mm.

Fig. 3.—Fragment of mucous sheath of *C. mitsukurii* from egg mass of *Charybdis erythrodactyla* from Society Islands. Scale 1 mm.

Fig. 4.—Basis and stylet of *C. coei*. Drawn from a safranin-stained section. Scale 0.03 mm.

Fig. 5.—Anterior cirrus of a free-swimming larva of *C. c. imminuta* showing its multipartite nature. Freehand sketch under oil immersion.

Fig. 6.—Cross section of a lapillus and sheath of *C. c. imminuta*. Stained with Delafield's haematoxylin and eosin. Scale 0.1 mm.

Fig. 7.—Anterior end of mucous sheath of *C. c. imminuta* from *Callinectes sapidus* at Grand Isle. A crab egg is shown beside the sheath. Scale 0.5 mm.

Fig. 8.—Eight-celled stage of *C. c. imminuta*. Scale same as for fig. 10.

Fig. 9.—Sketch of cephalic muscle fibers in region of rhynchodaeum in *C. mitsukurii*. The anterior end is directed toward the bottom of the drawing. Stained with Heidenhain's iron haematoxylin. Scale 0.05 mm.

Fig. 10.—Four-celled stage of *C. c. imminuta*, lateral view. Scale 0.05 mm.

Fig. 11.—Mucous sheath of *C. c. carcinophila* from *Ovalipes ocellatus* at Buzzard's Bay, Mass. Scale 1 mm.

Fig. 12.—Posterior region of sheath shown in fig. 7. Same scale.

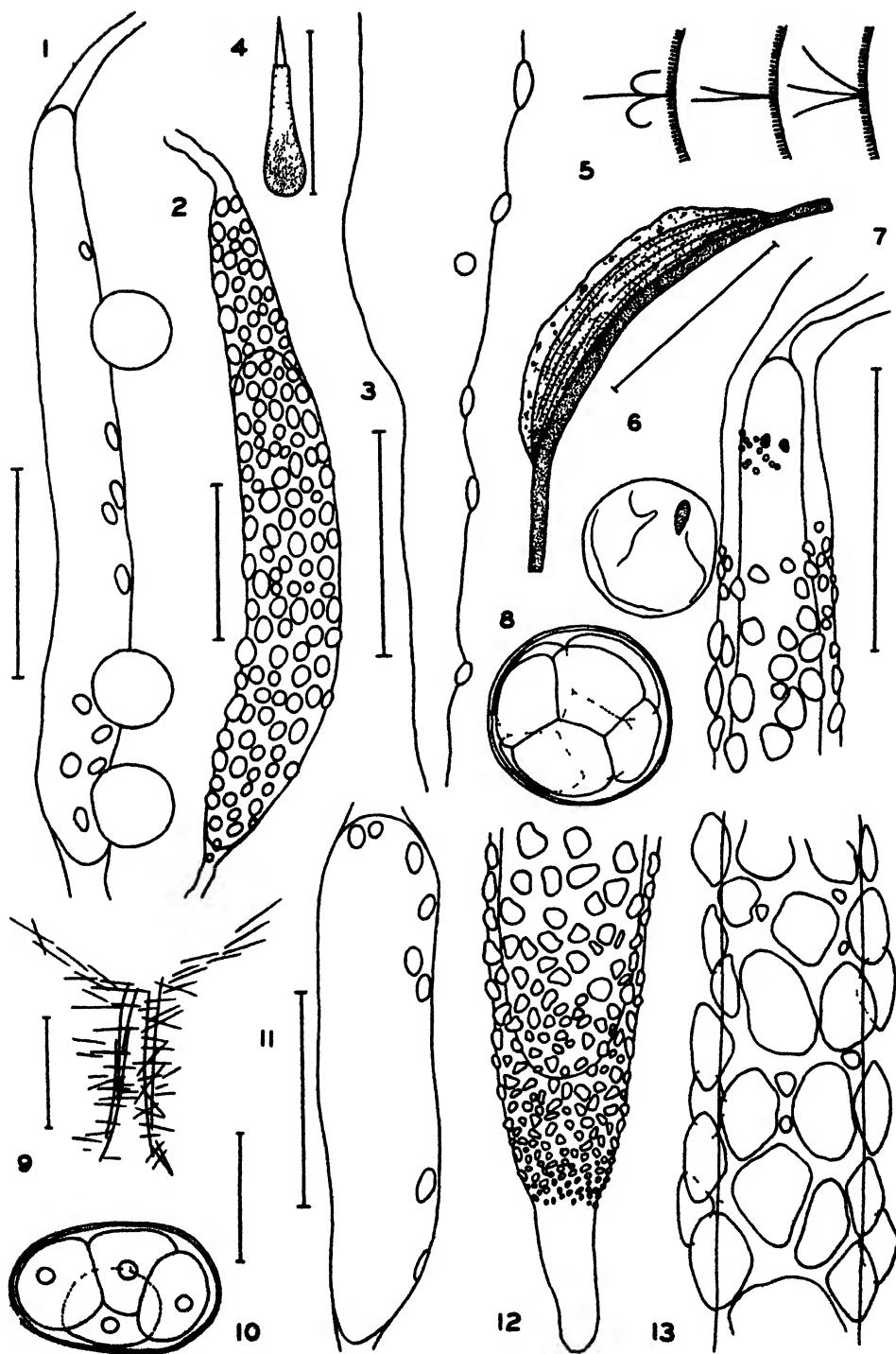Fig. 13.—Middle region of sheath shown in fig. 7. Same scale.

PLATE I

PLATE II

Fig. 14.—Cross section of a mature male *C. c. imminuta* in the region of the vas deferens. Scale (upper one on plate) 0.1 mm.

Fig. 15.—Sagittal section of the posterior end of a mature male *C. c. imminuta*. Scale (upper one on plate) 0.1 mm.

Fig. 16.—Sagittal section of the anterior end of a mature *C. c. imminuta*. Scale (lower one on plate) 0.1 mm.

Fig. 17.—Cross section of a mature female *C. c. imminuta* in the region of the ovaries. Scale (upper one on plate) 0.1 mm.

Fig. 18.—Cross section of a mature male *C. c. imminuta* in the region of the seminal vesicle. Scale (lower one on plate) 0.1 mm.

Fig. 19.—Cross section of a specimen of *C. c. imminuta* not sexually mature. Scale (upper one on plate) 0.1 mm.

Abbreviations

A......anus
AC.....anterior proboscis chamber
AE.....anterior part of esophagus
BA.....basis
BC.....posterior blood vessel commissure
BO.....anterior blood vessel commissure
CG.....cephalic glands
CM....circular muscle fibers
DC.....dorsal commissure of brain
GL.....gland cells in region of basis
I.......intestinal wall
IN.....integumental epithelium
LN.....lateral nerve cord
LV.....lateral blood vessel
MC....middle proboscis chamber
NC.....posterior nerve commissure

O..... egg
P.......parenchyma
PC.....posterior proboscis chamber
PE.....posterior part of esophagus
R......ridge of cells along vas deferens
RH.....rhynchodaeum
S.......spermatozoa
SG.....submuscular glands
SV.....seminal vesicle
T......testis
VC.....ventral commissure of brain
VD.....vas deferens
VE.....vas efferens
W......wall of ovary with developing eggs and yolk granules
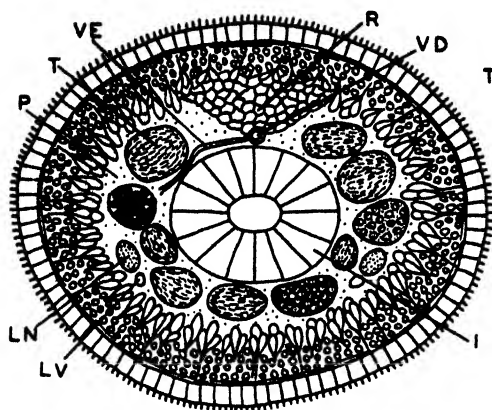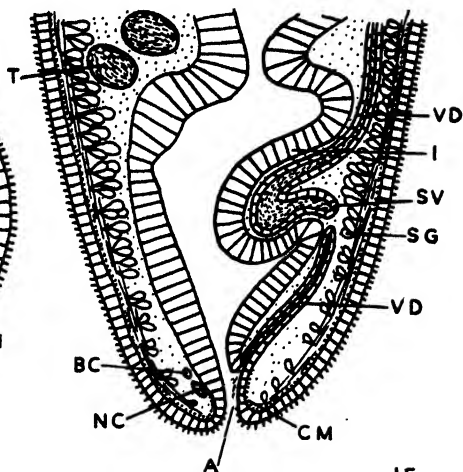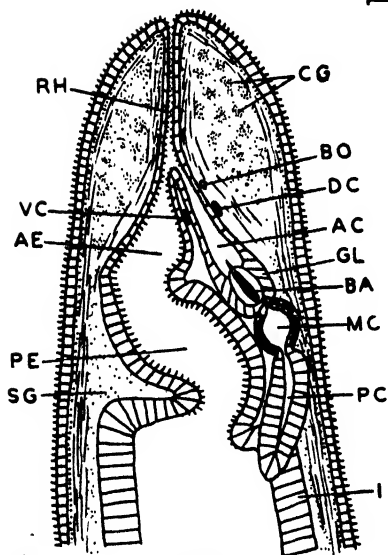
PLATE II
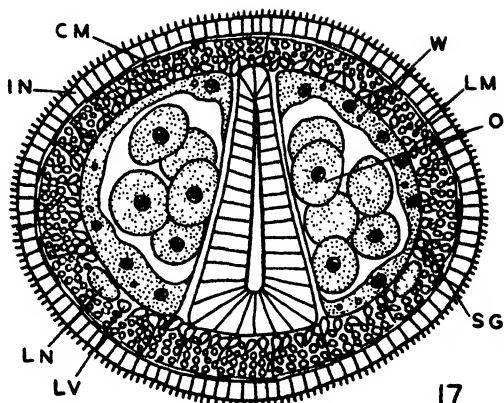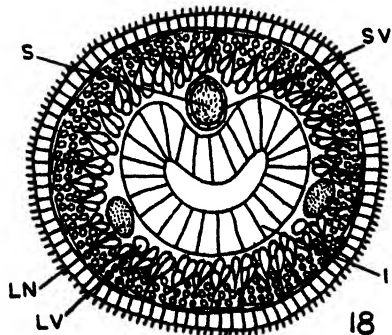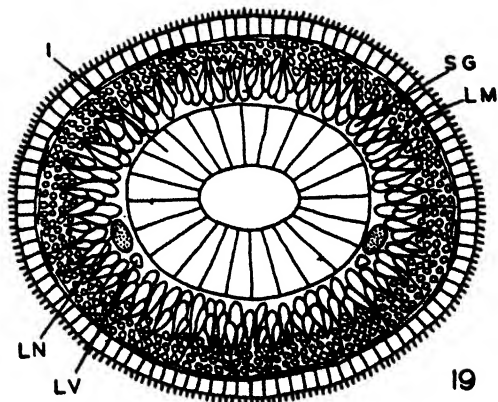
PLATE III

FIG. 20.—Immature specimen of *C. c. imminuta*, 0.273 by 0.084 mm. Scale 0.05 mm. Abbreviations same as for Plate II, except for the following: *AB*, anterior blood vessel commissure; *B*, lobe of brain; *O*, ocellus; *ON*, ocellar nerve; *R*, rhynchodaeum; *S*, stylet.

FIG. 21.—Part of an egg cord of *C. c. imminuta*. Scale 0.5 mm.

FIG. 22.—Outline of a longitudinal section of a sexually mature female *C. c. imminuta*. Scale 2 mm.

FIG. 23.—Outline of a longitudinal section of a sexually mature female *C. coei*. Scale same as for fig. 22.

FIG. 24.—Mucous sheath of *C. epialti* from *Euphylax dovii*. Scale 0.5 mm.

FIG. 25.—Free-swimming larva of *C. c. imminuta*. Scale 0.05 mm.

FIG. 26.—Arrangement of ovaries in a longitudinal section of *C. c. imminuta*. Scale same as for fig. 33.

FIG. 27.—Outline of basis of *C. c. carcinophila*, as seen in section. Scale same as for fig. 31.

FIG. 28.—Outline of basis of *C. epialti*, as seen in section. Scale same as for fig. 31.

FIG. 29.—Outline of basis of *C. mitsukurii*, as seen in section. Scale same as for fig. 31.

FIG. 30.—Cross section of basis of *C. c. imminuta*. Scale same as for fig. 31.

FIG. 31.—Outline of basis of *C. c. imminuta*. Scale 0.02 mm.

FIG. 32.—Mucous sheath of sexually mature female *C. c. imminuta*, 1.665 by 0.177 mm. Scale 0.5 mm.

FIG. 33.—Arrangement of ovaries in longitudinal section of *C. coei*. Scale 0.6 mm.

FIG. 34.—Smallest sexually mature female *C. c. imminuta* seen, 0.420 by 0.098 mm. Scale 0.2 mm.

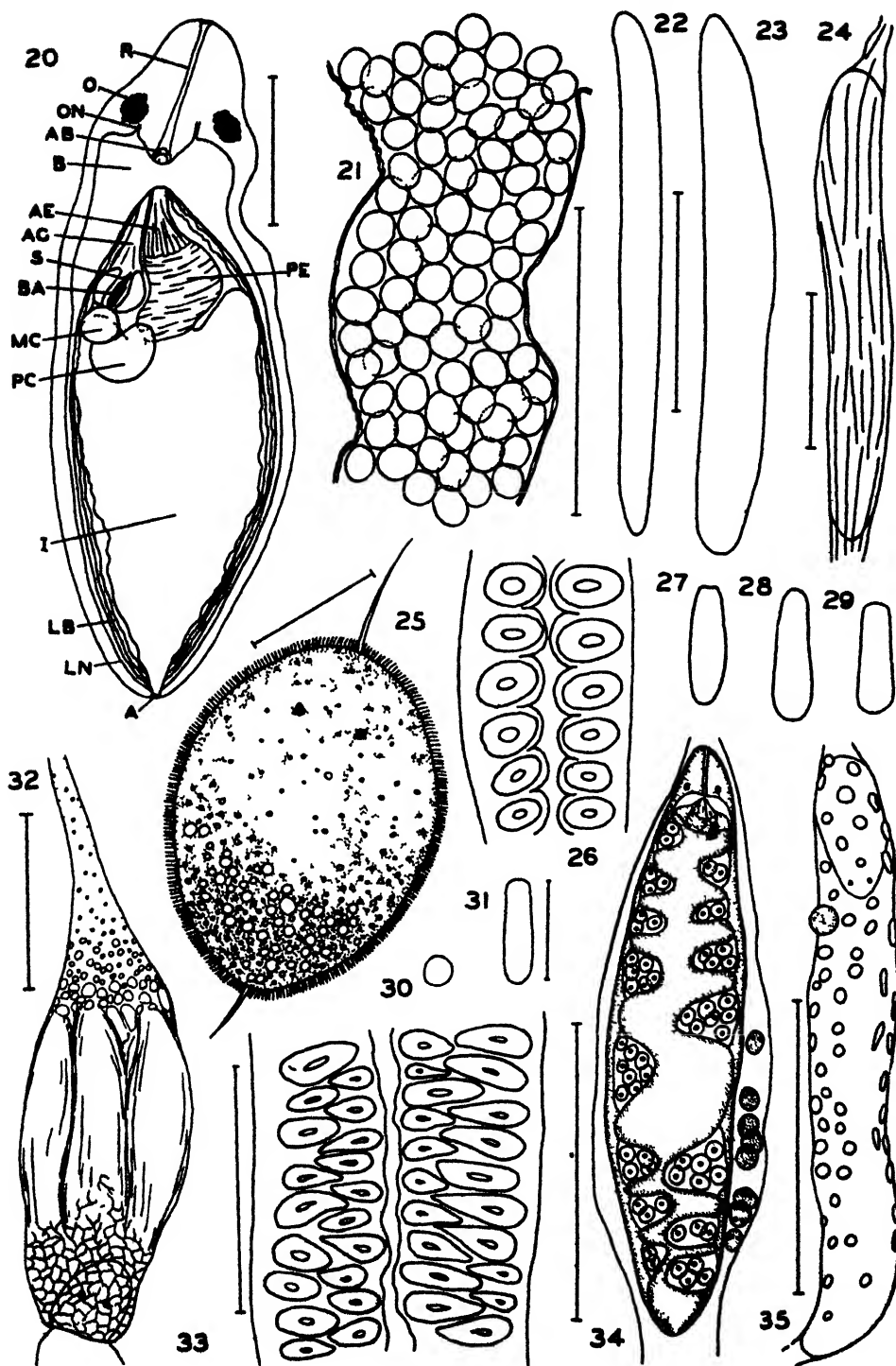FIG. 35.—Mucous sheath of *C. coei* from *Charybdis natator* at Zanzibar. Scale 3 mm.

PLATE III

PLATE IV

Fig. 36.—Basis, stylet, and surrounding cells in *C. c. imminuta*. Scale 0.02 mm.

Fig. 37.—Unfertilized egg of *C. c. imminuta*. Scale same as for fig. 10.

Fig. 38.—One-celled stage of *C. c. imminuta*. Scale same as for fig. 10.

Fig. 39.—Four-celled stage, polar view, of *C. c. imminuta*. Scale same as for fig. 10.

Fig. 40.—Part of a cross section of an adult male *C. c. imminuta* in the region of the vas deferens. Treated with Feulgen's nucleal reaction. Scale 0.025 mm. Abbreviations same as for Plate II, except for the following: L, longitudinal muscle fiber; S, nucleus of submuscular gland cell.

Fig. 41.—Part of a mucous sheath of *C. mitsukurii* from *Charybdis erythrodactyla* from the Society Islands. Scale 0.5 mm.

Fig. 42.—Outline of the body of a living specimen of *C. c. imminuta*. Scale 5 mm.

Fig. 43.—Basis and stylet of *C. c. imminuta* drawn from living worm. Scale 0.025 mm.

Fig. 44.—Late embryo of *C. c. imminuta*, nearly ready to rupture egg membranes. Scale same as for fig. 10.

Fig. 45.—Two-celled stage of *C. c. imminuta*. Scale same as for fig. 10.

Fig. 46.—Blastula of *C. c. imminuta*. Scale same as for fig. 10.

Fig. 47.—Contents of intestine of a living *C. c. imminuta* taken from a dark brown egg mass. Scale 0.05 mm.

Fig. 48.—Dorsal view of the posterior end of an adult male *C. c. imminuta*. Scale 0.25 mm. Abbreviations same as for Plate II.

Fig. 49.—Ovary of *C. c. imminuta* from which eggs have been shed. Scale 0 1 mm.

Fig. 50.—Anterior end of *C. c. imminuta*, showing esophagus partly protruded. Scale 0.25 mm.

Fig. 51.—A, B, and C are sketches of extruded esophagus of *C. c. imminuta*. The arrow shows the direction of peristaltic movements.

Fig. 52.—Anterior end of *C. c. imminuta*, showing partly protruded esophagus. Scale same as for fig. 50. Abbreviations same as in Plates II and III.
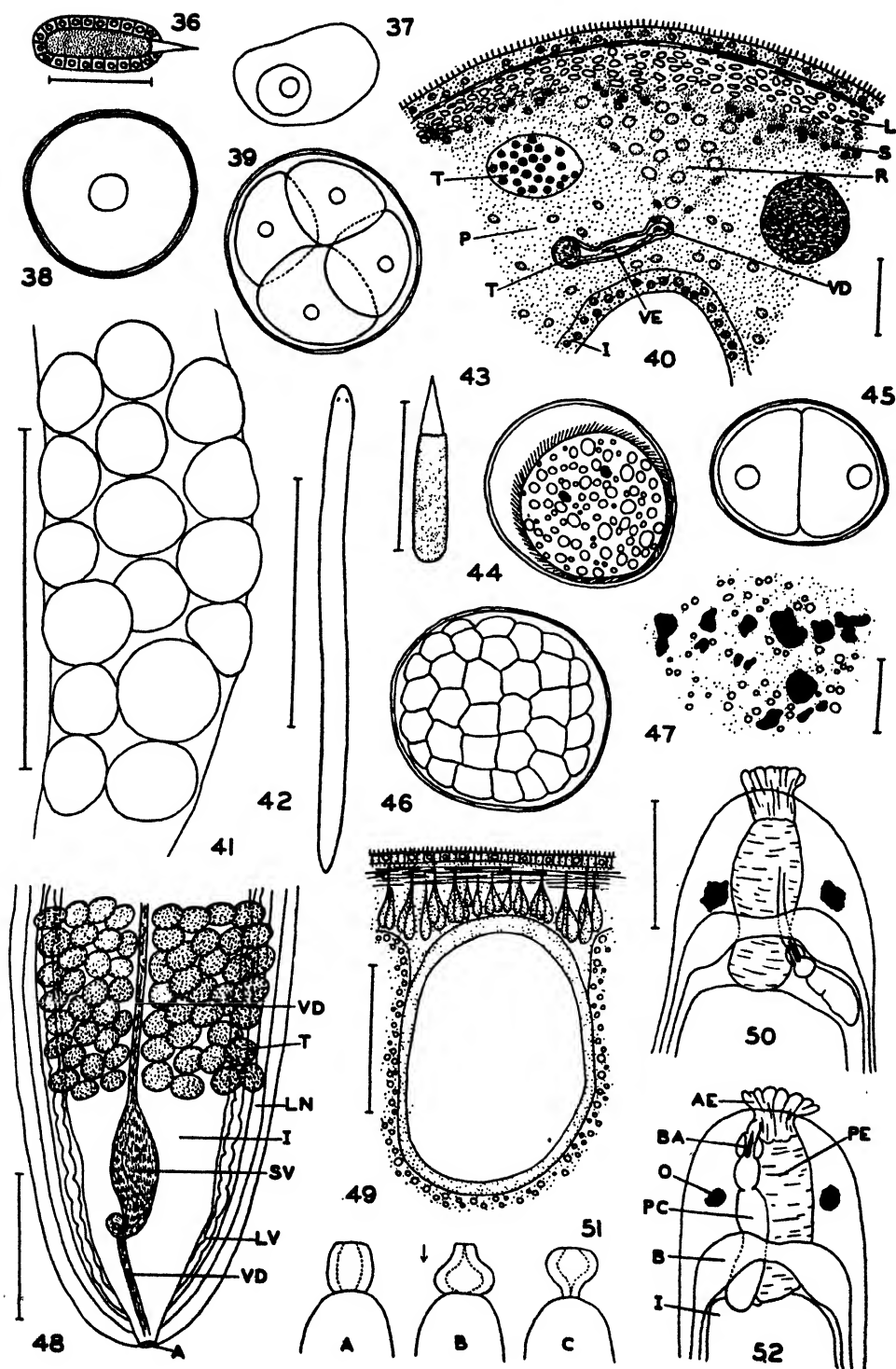
PLATE IV